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United States Department of the Interior, Oscar L. Chapman, Secretary
Fish and Wildlife Service, Albert M. Day, Director

SURVIVAL STUDIES OF BANDED BIRDS

By Joseph J. Hickey

A cooperative study of the U. S. Fish and
Wildlife Service and the Department of
Wildlife Management, University of Wisconsin

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TABLE OF CONTENTS

	Page
Preface	1
<u>Part I. Critique on Methods</u>	
Chapter I. Anatomy and Basis of Life Tables	3
Chapter II. Difficulties in Constructing Life Tables for Birds	13
Chapter III. Characteristics of Avian Life Tables	27
<u>Part II. Explorations in Population Dynamics of Representative American Birds.</u>	45
Chapter IV. Pelecaniformes (Double-crested Cormorant) . .	46
Chapter V. Ciconiiformes (Black-crowned Night Heron) . . .	57
Chapter VI. Anseriformes (Mallard and Redhead)	62
Chapter VII. Falconiformes (Marsh Hawk)	83
Chapter VIII. Charadriiformes (Caspian Tern)	88
Chapter IX. Columbiformes (Mourning Dove)	101
Chapter X. Strigiformes (Barn Owl and Great Horned Owl) .	108
Chapter XI. Passeriformes (Blue Jay)	119
<u>Part III. Implications of Mortality Data, with Special Reference to the Mallard</u>	
Chapter XIII. Indices of Mortality, Hunting Pressure, and Populations	125
Chapter XIV. Variations in Mallard Mortality Rates . . .	136
Chapter XV. Dynamics of Mallard Populations	154
<u>Appendix I.</u>	164
<u>Literature Cited.</u>	165



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PREFACE

This report is the outcome of a cooperative venture. For more than a quarter of a century, professional and amateur ornithologists (especially the latter) have been banding birds on a gigantic scale in North America. These banders laid the foundation of this research.

Since 1922, the U. S. Fish and Wildlife Service (formerly the Bureau of Biological Survey) has issued bird bands and kept the records. The clerical work in routinely accepting each letter about the discovery of a dead banded bird and converting this report onto an IBM record card takes about 19 minutes; many letters take even longer. Thus, in full cooperation with the Canadian Government, the Fish and Wildlife Service has erected an invaluable superstructure for ornithological research. Their investment in this report is very large.

My studies of the North American banding files were made possible from August 1, 1946, to December 31, 1947, by a fellowship of the John Simon Guggenheim Memorial Foundation, to which I want to extend my very sincere thanks. The project was carried out with the much-appreciated advice of Dr. Josselyn Van Tyne of the University of Michigan. Most of the work was done at the Patuxent Research Refuge (Laurel, Maryland) of the Fish and Wildlife Service. J. W. Aldrich, Clarence Cottam, F. C. Lincoln, A. L. Nelson, and G. A. Swanson, officials of the Service at that time, were unfailing in their encouragement and assistance. Other biologists then at Patuxent, D. L. Allen, L. M. Dargan, L. M. Llewellyn, J. P. Linduska, A. C. Martin, Neil Hotchkiss, R. E. Stewart, and W. H. and Lucille Stickle, helped me in less direct but much-appreciated ways. In the banding office, C. S. Robbins introduced me to the record files, and throughout my stay Mrs. Lois Smith Horn cheerfully and patiently advised me on clerical problems that were constantly arising. Others who helped clarify banding data were F. A. Carpenter, M. C. Hammond, A. S. Hawkins, C. M. Herman, H. A. Hochbaum, E. R. Jones, C. S. Jung, F. C. Lincoln, E. A. McIlhenny, A. G. Niss, R. H. Norr, M. D. Purnie, W. H. Ransom, LeRoy Wilcox, C. S. Williams, and V. T. Wilson.

The final preparation of the report was greatly aided by the University of Wisconsin. I am indebted to the late Professor Aldo Leopold who encouraged me to continue the study as a Department of Wildlife Management project, and to Miss Patricia Murrish and Miss Ruth L. Hine who typed innumerable drafts and carried out check calculations.

R. P. Allen, J. T. Emlen, Jr., A. S. Hawkins, Irving Kassoy, J. C. Neess, R. A. McCabe, L. K. Sowls, A. W. Stokes, and D. R. Thompson were kind enough to read various chapters as the report was in preparation.

Finally, I want to acknowledge the very great help of my wife, Margaret Brooks Hickey, who spent 11 months at Patuxent Refuge checking records and punching IBM cards, and who later contributed so generously of her energy in editing the manuscript in its final stages.

This manuscript was virtually completed on March 31, 1949. Minor changes including cursory references to subsequent literature were made up to December 31, 1951.

PART I. CRITIQUE ON METHODS

Chapter I.--Anatomy and Basis of Life Tables

This report is an exploration into the population dynamics of ten North American birds. The basic materials are literature on the productivity of these species and survival records maintained in the banding files of the United States Fish and Wildlife Service. Because the use of life tables in ornithology is still relatively new, the present study reviews the assumptions underlying such analyses--then proceeds to balance our present knowledge of productivity against the availability of mortality data on representatives of eight orders of birds. All too often, the samples finally proved to be too small, but the mallard does offer a rapidly increasing wealth of data for the student of vital statistics. In the case of this species, I hope this report will demonstrate the wide variety of indices into which modern banding data can be converted.

The present study is an ecological one, not a statistical treatise. No attempt has been made, for instance, to allocate sampling errors in such matters as the computation of seasonal recovery rates or to devise tests of significance for differences between some of the complex mortality series obtained from banding records. These still invite special studies. Despite their omission here, the report that follows is not an easy one to read, at least for biologists. For years, ornithologists have been compiling statistics on the numbers of eggs in birds' nests, on the percentages of successful nests, on the number of young per brood, and on the ages at which individual birds die. To interrelate these into crude but meaningful life equations for the best-studied species now requires effort and diligence. It is my conviction that these new pathways of the mind will in time lead us to broad vistas where multitudes of formerly unrelated facts will at last merge into logical perspectives, and the struggle for existence by each species will be more clearly visible. One such pathway is traversed here. The clearing away of boulders will, I hope, make it easier for others to follow.

History

The term life tables can be applied to tabulations of populations according to age groups. These summaries of the age structure of various species suggest to the geneticist and the evolutionist the rate to which natural selection may cull out mutations or permit them to become predominant. To medical men, life tables often disclose advances and weaknesses in public-health programs. From them ecologists can gauge environmental forces, fisheries workers can estimate future catches, and game managers appraise productivity and hunting regulations. In a real sense, they bridge the gap between the older biology and the new.

Life tables had an early origin which may never be satisfactorily fixed. By the third century they included calculations of "life expectancy" (Trenerry 1926). Their crude revival in the seventeenth century by John Graunt at once demonstrated that mortality is high in the early years of human life and that regularity exists in vital phenomena superficially seeming to occur at random (Pearl 1941, p. 25). Their present detailed state of description for human populations is well known to most readers, and a review of it is beyond the scope of the present paper.

No complete life table for a wild species appears to have been published until 1921 when Pearl and Parker reported on laboratory studies of the fruit fly (Drosophila melanogaster). Biology still awaited the success of field workers in marking, aging, censusing, and sampling wild populations. Fourteen years later, when Pearl and Miner (1935) reviewed the survival literature for the lower organisms, the house mouse (Mus musculus) was the only vertebrate to merit their attention.

The dam was now ready to burst. During the next dozen years, fairly intensive survival studies were published on a number of fishes, on 5 species of mammals, and on at least 15 species of birds. This work has been the subject of a recent and excellent review by Deevey (1947), so that a summary of it need not be repeated here. The review, modestly entitled an introduction, condenses both vertebrate and invertebrate survival material into life tables which, for the first time, permit comparative studies of the vital statistics of natural populations. A few of its salient conclusions are worth noting here.

"Both in nature and in the laboratory," writes Deevey (1947), "animals differ characteristically in their order of dying." These differences in survival, he points out, conform to or approximate three types of survival curves predicted by Pearl and Miner (1935):

Concave J-shaped survivorship lines.--In mathematical parlance these are known as negatively skewed rectangular curves. They are believed to reflect the production of enormous numbers of eggs by a single female and extremely heavy mortality in the early stages of life. Although these curves undoubtedly are characteristic of many fishes and invertebrates, survival in the early stages of life is extremely difficult to record in nature with any marked degree of accuracy. The only approach to this negatively skewed curve thus far reported for birds is found in Deevey's reanalysis of Nice's (1937) work on the song sparrow.

Convex survival curves (positively skewed rectangular curves).--These represent a high degree of survival throughout life and heavy mortality at the end of the species' life span. Under modern public-health programs, man is changing his survival curve from the concave toward the convex type (Dublin and Lotka 1936). Dall bighorn sheep (Ovis dalli) studied by Murie (1944), the rotifer (Floscularia conifera)

observed by Edmondson (1945), and possibly a population of barnacles (Balanus balanoides) reported by Hatton (1938) represent three species which Deevey found to approach this type of curve (Figure 1).

Survivorship lines indicating constant mortality rates.— When the survivors at each age level are plotted on ordinary graph paper, this type of line is concave but not necessarily J-shaped; on semilogarithmic paper, however, it has the particular property of appearing as a straight line. Such a survival curve is typical of the adult stages for many birds, their mortality averaging about 320 per thousand per hundred centiles of mean life span (Deevey 1947). It has not been found, however, to hold strictly for all ages of a species' life. Indeed many of the species that Deevey grouped under this category may, when their complete span of life is finally reported, exhibit the convex type of curve described above.

Anatomy of life tables

Although life tables have been adequately explained by Glover (1921), Hill (1936), Pearl (1941), and by many other writers, a few introductory words about them at this point will help readers unfamiliar with the literature of vital statistics.

Life tables contain one or two categories of primary data and two or more categories secondarily derived from them. These categories have come to be identified with standardized symbols (Pearl 1941, p. 220) which are given below. In any extensive study of survival, the investigator will find symbols a useful type of shorthand in his analyses. In ornithology, the nomenclature of survival studies is still so inexact that I have found symbols indispensable to clear thinking.

The skeleton of a life table may be said to consist of four or more columns:

(1) The age, which is best stated as an interval, is often given in years but also in other intervals as convenient. This column in a life table can scarcely be confused with any other but is often symbolized by the letter x. In broad zoological studies, these intervals can be set up as fractions of a species' mean life span. In restricting my own investigation to birds, I have found age intervals of one year to be convenient.

(2) The number living at the beginning of each age interval in column x can readily be plotted as a life curve. This series is symbolized by l_x and is synonymous with survival curve, survival series, and survivorship line. In human statistics, the number alive at the start of age 0-1 is usually taken as 1,000,000 or 100,000. In ornithological statistics, it seems best when possible to convert the raw data as Deevey (1947) did, and start with a cohort of 1000. As oviparous animals, birds lend themselves well to tabulations starting with the

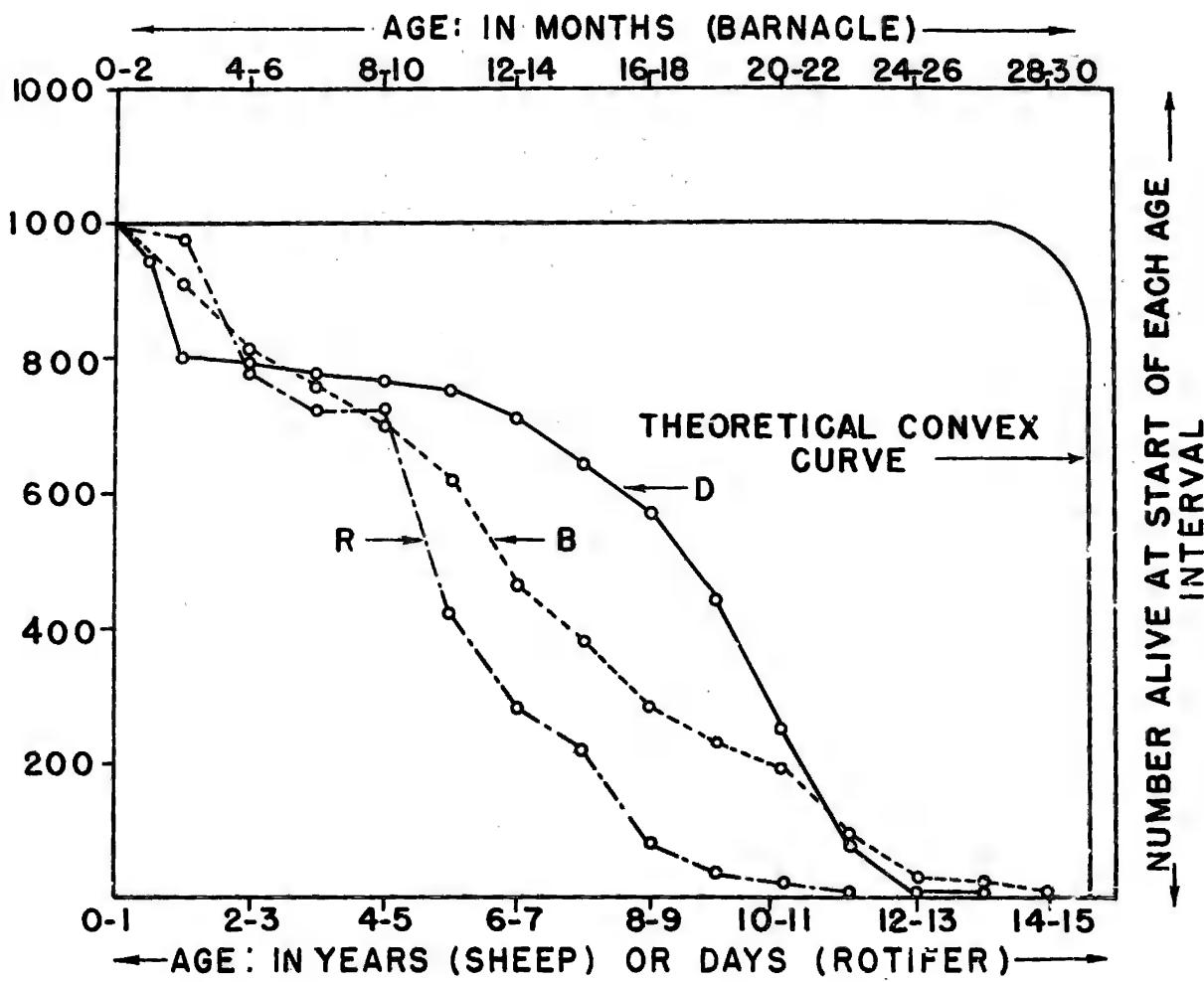


Figure 1.—Hypothetical convex curve and 3 survivorship curves which tend to approach it (after Deevey)
 R - a rotifer; B - a barnacle; D - Dall sheep

laying of fertilized eggs. Ornithological tables should, I think, also include data on the number of eggs that hatch, and in altricial birds the number of young that leave the nest. My own samples in this study were often so small that I avoided tabulating my results in terms of adjusted cohorts of 1000. To have done so would have magnified sampling errors and implied a far greater accuracy than is currently possible.

(3) The number dying within the age interval in column x is usually symbolized as d_x . The number of deaths is sometimes called a mortality series.

(4) The rate of mortality is the number dying in a given age interval divided by the number alive at the start of that interval. In avian life tables this result may be expressed as a percentage figure or as the number dying per 1000. In vital statistics, mortality rates are customarily symbolized as q_x ; these rates are far more precisely calculated for humans than any mortality rates thus far computed for birds. While some other symbol (like m_x) seems to me to be more appropriate for the crude results I have often obtained, I have followed other biologists in using q_x to identify mortality rates in this report.

(5) The mean after lifetime is the average length of life remaining to each individual alive at the start of a given age interval. The term is synonymous with "life expectancy," "expectation of life," and "complete expectation of life." In human life tables this column is often identified by the symbol \bar{e}_x . Pearl (1941, pp. 513-515) has given a helpful table for quickly ascertaining elapsed time between any two dates in the direct computation of mean after lifetime, as in Farner's (1945) work on the American robin. This method is not in itself a precise one in many ornithological life tables, because the monthly mortality reported on banded birds is not necessarily representative of unreported mortality in the same species. The dates on banding reports also contain other inaccuracies, which I will discuss later. Although Deevey (1947) has described an excellent short cut in computations of mean after lifetime, I have avoided calculating this statistic in the chapters that follow.

(6) Survival rate is not ordinarily found in life tables but is mentioned frequently in quantitative studies of bird populations. Where I have occasionally used it, it is designated by the symbol s_x . This of course is the same as $1 - q_x$.

Basis of life tables

Merrell (1946) pointed out at the AAAS meeting in Boston that life tables differ fundamentally in the way their primary data are gathered:

Dynamic life tables summarize the survival and mortality of a given cohort (or age class) over a period of years. One could set up such a table for native Americans born in the year, say, 1850, and

tabulate those alive at the start of each year from then up to the present. The amount of mortality each year would obviously be primary in nature, so that the annual mortality rates would be accurate and reliable, but only for this particular cohort. This type of table is seldom used in the vital statistics of human populations, because many of the data are essentially historical and because public health officials are concerned more with mortality statistics of the present. Dynamic life tables have, however, been utilized in survival studies of birds like the song sparrow (Nice 1937) and pheasant (Leopold, Sperry, Feeney, and Catenheusen 1943; Buss 1946), which were banded and, with varying success, retrapped alive in subsequent years. Deevey (1947) has termed such tabulations "horizontal life tables."

In time-specific life tables (termed "vertical tables" by Deevey) all the primary data are compiled from a single period of observation. An entire population may be available for study, as in a ten-year census of the United States (Glover 1921; Hill 1936), or when all the fish of a single lake are poisoned at the same time (Eschmeyer 1939; G. W. Bennett 1945). The age composition of bird populations has somewhat similarly been observed at specific times by study of banded samples. Michener and Michener (1933) have reported on the age distribution of house finches retrapped during a single month; Austin (1942) has shown the ages of common terns when they were retrapped on their nests; and Kortlandt (1942) has observed banded European cormorants by means of a telescope at their nesting colonies. The registered mortality data that now supplement census figures for human populations have no counterpart in the time-specific studies of wild animals. The mortality often cannot be readily inferred, since the age distribution of the living at a specific time is a function not only of the number of young produced in the past but also of mortality in previous age intervals. Mortality rates are therefore very difficult to compute in time-specific analyses of natural populations. O. L. Austin (1938, 1942, 1945, 1947a) has utilized this approach in his studies of the population dynamics of Cape Cod Sterninae. A comparison of his conclusions with those arising from a dynamic life table analysis is particularly instructive, but its presentation is postponed to a later section on the Laridae.

Composite life tables have occasionally been constructed from miscellaneous collections of mortality data that do not permit either dynamic or time-specific definition. Life expectancies (\hat{e}_x) have, for instance, been roughly computed for ancient Egyptians by Karl Pearson (1902) working with the age at death recorded on 141 mummy cases. In such a sample the individuals have been born in different years and have died in different years. Strictly speaking, the sample is neither a dynamic one nor a time-specific one. Although Dublin and Lotka (1935) state that "correct age specific rates cannot, of course, be computed on such a basis," I believe that this criticism really holds for a time-specific treatment of such data. The 141 persons can be studied as though they all were born at the same time. This assumption at once makes the population a hypothetical one, but

this departure from reality is certainly not much greater than in modern tables set up for a standard million persons. One can then claim that all 141 persons were exposed to the risk of death at the earliest age interval in the life table and proceed as Pearson did to compute mortality rates and expectations of further life.¹

When banded birds are recovered dead by the general public and reported to a central office, the mortality may be spread over many years just as the original dates of banding are. Lack (1943a, 1943b) was the first to take such mortality records and form a life table. The method seems similar to Pearson's (1902), and the results can be regarded as dynamic life-table analyses for hypothetical populations. In subsequent parts of the present report, this technique will be referred to as Lack's method.

Composite life tables have also been set up using a time-specific analysis instead. In these, mortality reports of banded birds have been grouped with survival reports to form life curves for the lapwing (Kraak, Rinkel, and Hoogerheide 1940), the European sparrow hawk (L. Tingergen 1946), and several other birds. This aggregation of mortality and survival will not yield reliable estimates of mortality rates that change with age (Chapter III). Nice (1937), Lack (*op. cit.*), Farner (1945), and others have shown, however, that in adult birds the mortality rate is reasonably constant for all ages. In such cases the method is a permissible one. Its limitations will be further discussed in a later chapter, and an example worked out solely from mortality reports is given in table 1.

¹Arne Fisher (1922, 1925) has claimed that it is possible to construct a human mortality table from a collection of death certificates and with no knowledge of the number of lives exposed to risk at various ages. His principal working hypotheses appear to have no present application in ornithological studies, and his attempt to reconstruct a time-specific life table from limited data has been coldly received by American mathematicians. In fact, one commentator at a Toronto meeting of the International Mathematical Congress made the very positive statement that any satisfactory results from Fisher's method would be due solely to the effect of pure chance.

Table 1.—Methods of Constructing a Composite Life Table -- I

Unchecked hunters' reports of adult mallards banded 1926-34 on the Pacific coast and shot in some subsequent year are here grouped together to show the results of two different methods of calculating annual mortality rate. When such rates would involve less than 100 alive at the start of an age interval, they were not calculated in this report.

Original Data		Dynamic Life-table Analysis			Time-specific Life-table Analysis		
		l_x	d_x	q_x	l'_x	d'_x	q_x
Age Interval (in Years)	No. Shot	Alive at Start	Number Deaths	Mort. Rate per Year	Alive at Start	Calcu- lated Deaths	Mortality Rate per Year
x+1 to x+2	845	1411	845	59.9	845	561	66
x+2 to x+3	284	566	284	50	284	160	56
x+3 to x+4	124	282	124	44	124	52	42
x+4 to x+5	72	158	72	46	72	43	-
x+5 to x+6	29	86	29	-	29	0	-
x+6 to x+7	29	57	29	-	29	17	-
x+7 to x+8	12	28	12	-	12	5	-
x+8 to x+9	7	16	7	-	7	2	-
x+9 to x+10	5	9	5	-	5	2	-
x+10 to x+11	3	4	3	-	3	2	-
x+11 to x+12	1	1	1	-	1	1	-
TOTAL	1411	2618	1411	53.9*	1411	845	59.9*

*The mean mortality rate per annum, this is always the most statistically reliable mortality rate in an avian life table.

In this table I have used some Fish and Wildlife Service reports taken from hunters' letters as an illustration of the two methods of analyzing a composite life table. Most of these birds were banded during the hunting season by A. J. Butler at Chilliwack, B.C., and by personnel of the Malheur National Wildlife Refuge at Voltage, Ore. First-year recoveries were not included in this table. These birds were unaged at the time of banding; their ages in the table therefore run x+1, x+2, etc.

Lack's method has the disadvantage of requiring a number of years to elapse before the life table can include the results of a given banding operation. The method makes for small sample size because recent banding work will not give data on the full life span of many species. This can be circumvented by expressing deaths for each age interval as a percentage of the number of banded birds available. Such a device tends to reduce sampling errors in the early age intervals. It is illustrated in table 2. The percentage results are, of course, expressed as birds dead or alive per 100 banded, and in succeeding chapters I will frequently convert such statistics to the number per 1000 banded birds available for study.

Table 2.—Methods of Constructing a Composite Life Table -- II

This hypothetical set of data illustrates how percentages (or their equivalent) can be used to set up a life table. Both dynamic and time-specific analyses are possible, but only the former is carried out here. Mortality rates are given as per cent per annum, age intervals as years.

	Year Banded	Number Banded	Year Reported Dead				Total No. Dead
			1940-41	1941-42	1942-43	1943-44	
I Original Data	1940	1000	100	30	10	3	143
	1941	1000	-	95	25	11	131
	1942	1000	-	-	100	20	120
	Total	3000	100	125	135	34	394
II Same Data on Age- Interval Breakdown	Year Banded	Number Banded	Number 0-1	Reported 1-2	Dead 2-3	by Age 3-4	Total
	1940	1000	100	30	10	3	143
	1941	1000	95	25	11	-	131
	1942	1000	100	20	-	-	120
	(d _x) Total	295	75	21	-	3	394
	(a) Number banded birds available per interval	3000	3000	2000	1000		
III Life Table*	(d' _x) % Reported dead	9.83	2.50	1.05	0.30	13.68	
	(l' _x) % Alive at start	13.68	3.85	1.35	0.30	19.18	
	(q' _x) Mortality rate	72	65	78	100	71	
	(d" _x) No. dead per 1000 banded birds available	98.3	25.0	10.5	3	136.8	
	(l" _x) No. alive at start per 1000 available	136.8	38.5	13.5	3	191.8	
	(q" _x) Mortality rate	72	65	78	100	71	

* $d'_{x'} = d_x/a$. This technique was independently worked out only in the present study but also by Edward G. Wellein (unpubl. ms.), by Bellrose and Chase (1950), and by Paludin (1951).

Extent of avian life tables

Ornithological life tables can also be classified according to the thoroughness with which they span a bird's entire life. Complete life tables include survival data on eggs, nestlings, fledglings, sub-adults, and adults. During the fall of 1947, Mrs. M. M. Nice generously reworked her field data on the song sparrow and helped me construct such

a life table for this species. The result differed slightly from one constructed by Deevey (1947) from Nice's published data (1937). Many of Mrs. Nice's observations were concentrated on the first and second broods of this species; a precise picture of reproductive success in later broods is still needed.

Abridged life tables cover only a part of the life span of a species. The term usefully distinguishes those that involve only the subadult and adult stages of a bird's life. Such life tables, in varying form and with varying amounts of data, are found in the reports of banders who retrap birds over a period of years; they also are represented in the composite life tables that have been described above and that form the main basis of the present study.

Summary

Although life tables have long been used to summarize vital statistics, data for wild populations have become available only within the last twenty years. An important component of them is the survival curve, which tends to be either concave and J-shaped (teleost fishes, song sparrows) or convex (Dall sheep, rotifers); an intermediate type (straight-lined on semilogarithmic paper) involves constant mortality rates for successive age intervals and typifies the adult stages for many birds. The columns of a life table give it a definite and useful structure. In this paper, such a table is said to be a dynamic one when all the animals are born in the same period; it is time specific when both survival and mortality data are gathered in a single period--and the animals are born in different periods. Centralized banding files yield an intermediate type, called a composite life table in this report. Life tables may be further identified as complete or abridged. The former is still very rare in ornithology; the latter type, covering only the subadult and adult stages of a bird's life, comprises the main subject of the present investigation.

Chapter II.--Difficulties in Constructing Life Tables for Birds

In theory a life table ought to start with the zygote. In practice, such an ideal is virtually impossible to attain at this time, especially in viviparous and ovoviviparous animals. In our most studied species, man, fertilized ova less than ten days old are still unknown to science (Arey 1944, p. 139). Taussig (1936) in her classic treatise on abortion demonstrated the unreliability of published data on intra-uterine mortality. She assumed that in United States cities one abortion (premeditated or unpremeditated) occurred to every 2.5 deliveries, and that in rural districts this ratio was 1 to 5. More recently, Arey (1944, pp. 133-134) has estimated that about one pregnancy in 4 is unsuccessful, largely because the embryos are not vigorous enough to reach birth as living individuals. Perry (1945) in his careful study of brown rats (*Rattus norvegicus*) found intra-uterine mortality to amount to about 10 per cent. It is obvious that, from a purely biological point of view, mammalian life tables, including the modern actuarial tables for man, are still incomplete. The research of ornithologists on early mortality in each species is clearly less complicated, although still beset with difficulties.

Real versus theoretical populations

The construction of an avian life table depends on special and diverse research opportunities that are not always given to the same investigator. Mortality in the egg and nestling stages of the caspian tern can, for instance, be investigated by a single person at one or more colonies. In this species, however, a low rate of recovery of banded birds requires such a large-scale banding program that compilation of mortality data on the adult stages of life almost certainly will require the field work of many banders over a long period. Life tables for birds ideally should result from single well-coordinated research projects, but their present scarcity encourages the construction of synthetic tables derived from a mosaic of reliable data obtained from diverse sources. These synthetic tables of course represent theoretical populations. A theoretical population, however, is the one most frequently encountered in all life-table work. Whenever an investigator computes an average, as of the per cent of eggs hatching in a 3-year study period, or of adults returning in a 5-year trapping program, this statistic departs from reality. It is not the product of what occurred in a given year but the composite product of what happened in several years. In effect, it holds for a theoretical population rather than for a real one. Failure to appreciate this point has frequently confused students with whom I have discussed life-table results. This confusion is particularly associated with mortality rates for adult birds.

Life tables by Kraak, *et al.* (1940), Lack (1943a, 1943b) and others emphasize that a constant annual mortality rate exists throughout the adult birds' life. One is tempted to ask: Do not severe and atypical winters bring about wide fluctuations in adult mortality rates? The answer is that they do; but they operate on real populations, not

theoretical ones. The winter of 1933-34, for instance, was so severe in the northeastern part of the United States that Lake Ontario and Long Island Sound both froze over. Mortality rates in a cohort of herring gulls banded in, say 1928, would be governed by this disastrous weather (table 3). But in a sample of birds banded from 1925 to 1941, the effects of this winter would be masked. Other winters, both severe and "open," would help create an average picture of mortality from 1925 to 1941, and the mortality rates would tend to become the product of all conditions. The final figures for adult mortality rates over a 20- or 25-year period would thus be representative of a purely theoretical population.

Table 3.—Variation in Herring Gull Mortality During Specific Years

Birds banded as nestlings and later found dead. Each year starts September 1. Notice the higher mortality reported in 1929-30 and 1933-34.

Year Banded	Year Birds Were Reported Dead																	
	'24	'25	'26	'27	'28	'29	'30	'31	'32	'33	'34	'35	'36	'37	'38	'39	'40	'41
1924	21	1	1	1	1	2	1	1	0	4	1	0	1	0	0	0	0	0
1925	-	32	6	2	3	4	2	0	0	3	1	0	0	0	0	0	0	0
1926	-	-	61	11	2	6	1	2	3	1	1	0	0	1	0	0	0	0
1927	-	-	-	60	3	6	4	4	7	2	0	0	1	1	0	0	1	1
1928	-	-	-	-	14	20	7	8	2	6	2	1	0	1	1	1	1	0
TOTAL																		
Dead					23	38	15	15	12	16	5	1	2	3	1	1	2	1
Alive at start					135	112	74	59	44	32	16	11	10	8	5	4	3	1
Mortality rate*					17	34	20	25	27	50	31	-	-	26	-	-	-	-

*Percent per annum

Under such circumstances, it seems to me proper at this time to combine the results of nesting studies (which yield survival data on eggs and young) with the results of banding analyses of subadult and adult survival--even though the field data may originate in different regions and from the work of different investigators.

Determination of fledgling survival

The early steps of an avian life table can only come from intensive studies of nesting populations. When one considers the large number of species available, surprisingly few of these studies have been published up to the present. One serious difficulty in working with many species is the frequent impossibility of following the young birds after they leave the nest. This is unfortunately complicated by the rapid breaking down of family ties among most of the smaller birds, and by the dispersal of the young from study areas (Sherman 1924; Nice 1937, p. 133). It is also paralleled by an important failure of the bird-banding technique to record accurately the mortality of these very young birds from predation, starvation, or the weather.

Nice (1937, pp. 180-189) has thoroughly reviewed the problem of determining survival of young passerines on intensively studied sample areas. Among house wrens (Kendeigh 1934), starlings (Kluijver 1935), and song sparrows (Nice 1937, p. 189), about 17 to 20 percent of the young that leave the nests apparently must survive to the next breeding season in order to keep the populations stable. These birds, Nice points out, are never all retrapped because only a substantial proportion of the survivors may return to the general vicinity. The manner in which the breeding density of these survivors decreases with distance from their birthplace is illustrated in figures 2 and 3. At least in migratory species having a reasonably wide variety of available habitats is which the young can nest for the first time, intensive observation and retrapping cannot give a reliable estimate of early survival.

Among those species in which family ties persist for some time, the observational handicaps are greatly reduced. Brood counts in waterfowl and many gallinaceous birds can often be extended over a period of many weeks. In cranes, swans, and geese, these family ties seem to persist over an entire winter (Heinroth 1911; Stevenson 1941); they are also prolonged in at least one of the titmice (Van Tyne 1948). Under such conditions, successive observations of the size of broods throughout the summer can yield reliable data on survival. This approach has been used on pheasants by Errington and Hamerstrom (1937), on blue-winged teal by L. J. Bennett (1938, pp. 73-74), and on redheads by J. B. Low (1945). Its limitations on diving ducks (in which hens frequently abandon their young) have been pointed out by Hochbaum (1944, p. 161).

There is a considerable difference of opinion as to the choice of starting date with which to compile mortality records of banded birds reported by the public. Paynter (1947) used July 1; Lack (1943a, 1943b, 1946a) used August 1; I have frequently used September 1; Farner (1945) used November 1; Kraak, Rinkel, and Hoogerheide (1940) used January 1; and Stuart (1948) March 1. It has now been shown that a starting date of August 1 in many passerine species does not exaggerate first-year mortality by giving the original banders a special opportunity to find dead fledglings (Lack 1946b). In a number of samples that I studied, August banding operations prevented me from starting the compilation at the first of that month. Both Paynter (1947) and Deevey (1947) seem to feel that life tables based on the banding of juveniles should start with the mean date on which the nestlings were banded. The choice of such a date seems to me to introduce sampling variables of unknown influence. Where a scientific station is located at or near a nesting colony, total mortality in the nestlings might be accurately recorded by the investigators. Once the birds disperse from the area, reports by the public constitute an entirely different type of sampling. I fail to see how the two types of data can be indiscriminately mixed and used to compute a first-year mortality rate. Where there is no scientific station nearby, the dead bodies of small-sized, very young birds are less evident to a casual observer than those of larger, adult birds. This is

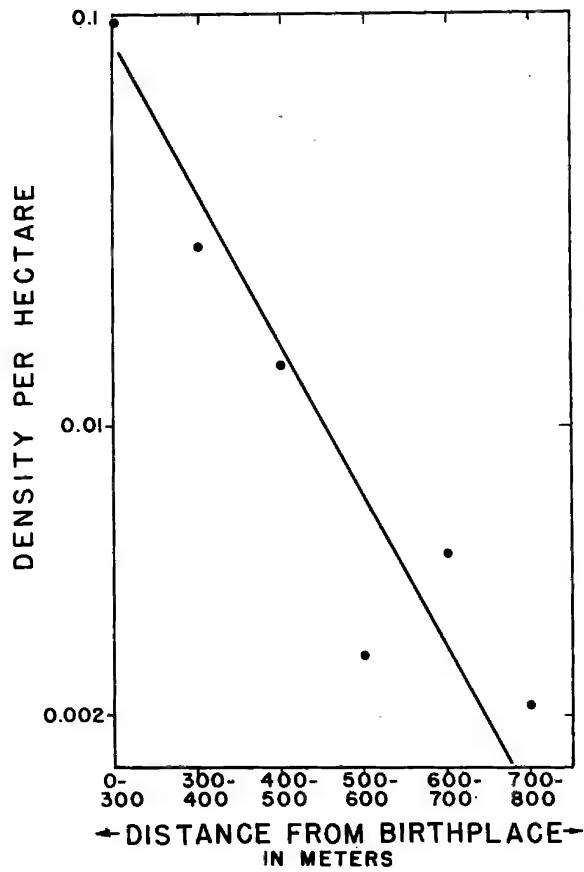


Figure 2

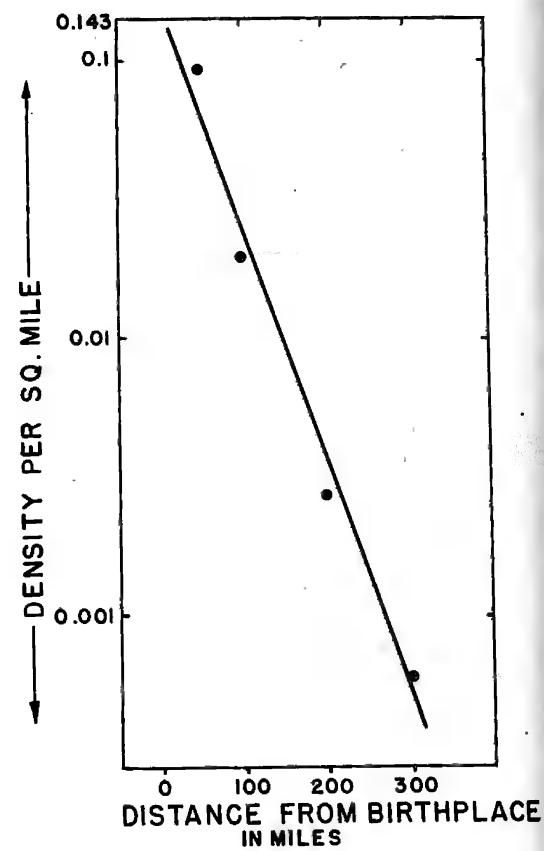


Figure 3

Figure 2.--Density of Fledgling-banded Song Sparrows as Retrapped a Year Later on and Near a Study Area (after Nice 1937). In this and the next figure, the "curve" has been drawn in by visual inspection.

Figure 3.--Density of Juvenile-banded American Robins Found Dead by the General Public in Some Subsequent Breeding Season (after Hickey 1943).

particularly true after predators or scavengers have worked over the corpses. This would potentially bias the resulting mortality reported.

Lack's (1946b) suggestion that January 1 should be used as the date from which to calculate the survival of birds on the basis of banding recoveries has been heartily seconded by Farner (1947) but is not followed in the present report. The use of January 1 will, of course, make more data available for the calculation of adult survival rates, but the determination of subadult survival should not be neglected. Lack (1946b) has demonstrated that in several species (European blackbird, song-thrush, and lapwing) the mortality rate decreases from the bird's first August 1 to the following January 1. Subadult mortality or survival rates therefore have considerable significance in the population dynamics of some species. In the larger birds, which are particularly vulnerable to gunners, subadult mortality rates derived from banding tend, however, to be somewhat biased. When a life table derived from banding data for such species can start close to the time the young birds leave their parents, the investigator is in a particularly good position to check the bias in his results against an analysis of nesting productivity. As I will show in Chapter III, this is also in many cases an all-important check on potential band loss.

Retrapping of adult birds

An immense amount of survival data on adult and unaged birds has been accumulated by the systematic retrapping of banded birds. The correct interpretation of these data depends on the banders themselves, as they are the only ones who can estimate annual variations in the intensity and efficiency of their own trapping activities. I therefore did not use survival data of this type when I encountered them in the centralized files of the Fish and Wildlife Service.

The accuracy of adult survival rates based on retrapping apparently varies from species to species. Although the migrational homing of adult birds is a generally accepted phenomenon, Nice (1937, pp. 176-178) has already shown that it may even vary between sexes and that it is poorest among species with specialized nesting sites. Even during the nesting season, when bird populations are relatively stationary, many adults that disappear from a study area are rather promptly replaced. These replacements must mean that the disappearance of an adult cannot always be safely taken as proof of its death, for the bird may have deserted and moved to a new location. Direct observation of this phenomenon during the nesting season has been reported by Green (1916), and circumstantial evidence has been gathered by various observers. Quantitative measurements of it are supplied for the song sparrow by Nice (1937, p. 173): In 6 years of observation, in which a total of 565 adults were present at the start of the nesting season, 123 birds disappeared in the next two months. The 37 birds that soon replaced these 123 represented 7 per cent of the original population. I believe that this 7 per cent is a rough measure of observational error in the study-area technique that Nice used, and that it could well be added to the percentage annually retrapped in an attempt to approximate annual survival rate of adults.

In a few species where banded adult birds are found dead during the nesting season by the general public, it may be possible to plot the distances at which they have been recovered from the original points of banding. This phenomenon should be explored for both robins and blue jays.

A third type of correction has been applied to retrapping data. In this, the number annually trapped has been compared to a census on the study area, and a correction made for untrapped residues of banded birds in the population. S. H. Low (1933, 1934) has thus converted return data into survival data for tree swallows nesting on Cape Cod, and Leopold, Sperry, Feeney, and Catenheusen (1943) and Buss (1946) have analyzed winter trapping results for ring-necked pheasants in Wisconsin. The validity of the correction factor here depends in part on local landscape and land-use conditions that permit the censused population to be identified as the sample being trapped. It also depends on the assumption that the banded birds always return to the study area.

Accuracy of bird-banding

The system of bird banding has so long been a valuable source of information to ornithologists that ordinary skepticism regarding its results seems almost out of place at this time. The program is known to work; the question is, how accurately?

Issuance of bands.--From 1922 to 1947 the U. S. Government has issued about five million bird bands. Of these, 10,000 (numbers B667000 to B677000) are known to have been issued in duplicate and presumably used in the field. This is an overall error of 0.2 per cent.

Retrapping by banders.--Since I made no studies of the survival of birds based on retrap work by banders, I did not appraise the accuracy of this type of research. When a bander retraps birds he has previously banded, perhaps only an eyewitness can check the carefulness of his work. When he reports the trapping of a bird ringed by another bander, the Fish and Wildlife Service has an opportunity to compare his report of the species and sex with that of the original bander. Discrepancies between such reports were fairly frequently discovered by Mrs. Lois Horn, of the Fish and Wildlife Service staff, during the time I worked at Patuxent. In the case of one veteran duck bander, 7 out of 8 "foreign" recoveries he reported in 1946-47 were either spurious numbers or credited to a different species by other ornithologists.

Banders' schedules.--Official forms (or schedules) are used by banders to report their work to the government. On the whole, the preparation of these seems to be good, the more inadequate record-keepers having been quickly "weeded out" through revocation of their banding permits. (A large part of one clerk's time in 1946-47 was still being spent, however, in clarifying the schedules of banders who should have been dropped years ago.) One regrettable failure of banders should be mentioned. This is the tendency to omit age and sex in their reports,

especially by not completing a line of ditto marks down a page. One of the best banding jobs ever done on the redhead duck lost much of its value because the bander gave neither the age nor the sex of the birds he banded in the summer of 1932.

In some cases the schedules now on file at the Patuxent Refuge represent third-hand (rather than second-hand) information. This condition is the product of an office operation called "reducing the files." Where two schedule pages for the same species are less than one-half filled out, clerks have occasionally copied the data from the second page onto the first. Many of these workers (apparently in the WPA) failed to transfer the year of banding as well. "File reduction" has not only made for such errors but it has been frequently characterized by failure to copy age and sex. I was unable to locate a sizeable fraction of the original schedules thus reduced. Because the schedules are always second-hand sources of data subject to typically human errors of transcription, it is regrettable that the Fish and Wildlife Service has never required its cooperators to turn over to the government their original records when their interest in the program has terminated. (This would at least permit the safekeeping of primary data by inexpensive microfilming.)

Reports by the public.--It is obviously rather difficult to test the accuracy of recovery data sent by the general public to the Fish and Wildlife Service. The amount of information supplied by laymen varies considerably. I noticed that about 12 per cent (in 1281 cases) failed to mention the places of recovery, over 10 per cent (in 1445) failed to specify the date of recovery, and that at least 33 per cent (in 373) were accompanied by enclosure of the band. In the fall of 1947, duck hunters were enclosing bands in about one-half of the letters received at Patuxent.

Two tests of the accuracy of numbers reported to it have been used by the Fish and Wildlife Service with varying degrees of consistency: (1) In some cases the species and sex cited in a recovery letter can be compared with the bander's data as to species and sex. In one series of 1445 Mallard cards, I found that there had been no follow-up in 12 cases (0.8 per cent) where bander and hunter differed as to sex. In this same series, some hunters differed with the bander's report as to the species involved. The significance of the latter discrepancy is, of course, debatable. (2) In other cases, the Service has used a screening test of geographic implausibility. A New York-banded greater scaup shot on the Pacific coast would fall into this class. (One actually did.) A yellow palm warbler recovered in Newfoundland in November, 52 days after it was banded on Cape Cod (Lincoln 1939: 137) would be another example. Reports like these are usually followed up by requests that the band be shipped to the Service.

Among 375 letter writers who enclosed bands, I noted that 25 mentioned the band number correctly in their letters, 25 wrote the number without giving the serial prefix (40, 41, 42, etc.), and one mentioned

the band number incorrectly. In another series of 250 letters with no band included, the clerks had promptly spotted 5 numbers that contained an obvious error. The probabilities of plausible but erroneously reported numbers escaping detection vary from species to species. Among the mallard records that I examined most carefully, 0.5 per cent might be taken as a preliminary estimate.

Table 4.--Factual Discrepancies in Fish and Wildlife Banding Cards

Discrepancy	Methods of Eliminating Discrepancy					
	Chiefly Checking Machine Banders' Reports		Checking Fiscal Yr. Rec'd	Checking Recovery Minor	Original Error	Reports Major Error
	Sorting	Reports	Yr. Rec'd	Minor Error	Major Error	
	Number Errors per 1000 cards					
Wrong species	0.5	1.5	-	-	-	-
Spurious record	1.4	0.7	-	0.7?	0.7	
Wrong banding date						
Year	1.5	2.5	-	-	-	-
Month or day	-	33.0	-	-	-	-
"How obtained" guessed	-	-	-		29.1	
Date of recovery						
Omitted in letter; guessed on card						
As "about"	-	-	-	93.5	-	
As "season"	-	-	-	8.3	-	
As definite date	-	-	-	16.6	-	
Made too definite	-	-	-	15.9	-	
Wrongly transcribed	0.7	-	1.4	13.2	-	
Banding age guessed	-	80	-	-	-	-
Sex						
Missing on card	-	20	-	-	-	-
Conflicting data	-	-	-		8.3	
Guessed by clerk	-	1	-	-	-	-
Wrongly transcribed	-	7	-	-	-	-
Questionable record	0.7	-	+	-	-	1.4
TOTAL	4.8	145.7	1.4+	147.5**	2.14*	

* Classification of major and minor errors depends in part on the use to which the recovery reports are put. For some investigators the source of a recovery report is of little interest, and the 29.1 guesses on "How obtained" would represent a minor error. The conflicting data on sex represents a type of discrepancy that might or might not be important.

Clerical transcription of data.--In table 4 I have attempted to summarize discrepancies and errors of transcription or interpretation on 2000 cards checked against banding schedules and 1445 cards carefully compared with letters of recovery. This test was based on mallards banded by a single person, A. J. Butler, in British Columbia; it followed up a much smaller test on 51 banders whose cards showed

similar types of errors. This table seems to me to be fairly typical of deviations encountered in the U. S. banding files, but the number of duplicate cards seems somewhat low in my experience with other blocks of cards. The need to check banders' reports, underemphasized by the table, is especially important where birds have been hand-reared. In one sample that I once gathered together for a life table, about half the birds subsequently proved to be of game-farm origin.

Verification in this study.—The frequency of minor discrepancies and major errors in the U.S. banding files imposes an intolerable burden on any investigator attempting to carry out a scholarly study. In one sample of nearly 2400 cards, 39 per cent of the letters could not be located for the years between 1930 and 1943. Recovery letters are filed by banders' names and in an approximate order of receipt. The task of verifying cards against these letters proved to be extremely time consuming. As I proceeded, I found that large blocks of cards shrank to a very small sample when one rigidly defined the type of recovery to be studied (as say, juveniles banded before September 1, or known adults not banded in the hunting season). To throw out 39 per cent of the cards because the dates of recovery could not be checked reduced most samples to levels of mathematical absurdity. This seemingly leaves one pinned on the opposing horns of a dilemma provided by the need for sound scholarship and mathematically based logic.

My solution of this problem was to use cards in spite of the failure to verify them against recovery letters, and to avoid drawing categorical conclusions so refined that they depended on the sex of a bird or the exact month it was recovered. The present report therefore contains no refined calculations of life expectancy (mean after lifetime) such as those computed by Farner (1945). In actuarial work, this failure might be serious. In animal population studies, it is often counterbalanced by satisfactory calculations of annual survival rates for subadult and adult classes. When direct computations of mean after lifetime consider the month in which each bird is reported to have been found dead, this date is slightly biased for large birds with conspicuous skeletal remains. It is frequently biased, too, by returns from hunters, and always depends upon the assumption that reported mortality occurs in the same monthly proportion as unreported mortality.

During the course of my work, I systematically tabulated recoveries according to the months alleged for each of them. Birds found dead could thus be compared with birds shot; those captured alive in Texas could be compared with those captured alive in Oklahoma, and so on. Thus, samples of equal bias were contrasted with each other. These comparisons in some cases approximate what is happening in nature; in many they may not. Their chief use in this study arose in the search for differences between types of recoveries. Even when recovery dates have been verified with extreme care, their monthly variation in highly migratory species may be importantly distorted by geographic variations in human literacy, language, and cooperativeness.

The Fish and Wildlife Service recovery cards contain one piece of information that I came to regard as being especially useful in sampling analyses of bird survival. This is the fiscal year in which each report is received. In the later stages of my study at Patuxent, I discarded from life tables all cards that showed a recovery date differing from the fiscal year received. This practice of using only reports sent in promptly had the following effects:

(1) It removed from each sample all reports in which the memory of the band recoverer is liable to error.

(2) If the clerk transcribed the year of recovery incorrectly (especially in the early days of January), the error was promptly caught and the card eliminated. (Fiscal year received is usually stamped on cards.)

(3) Samples for the more recent years are subject to less bias. Suppose, for instance, recoveries are carded and punched for those received through June 30, 1946. If the sample includes birds with the fiscal-year discrepancy, items for the year 1945 might be changed by reports received in, say, 1949 or 1950. Life tables of this kind thus tend to be more incomplete for the later years than they are for the earlier ones.

One tally kept on 801 waterfowl cards checked in this manner showed that 39 (4.9 per cent) were eliminated for this discrepancy; this test followed the removal of 25 duplicates. The percentage eliminated among non-game recoveries was probably lower.

Errors in tabulation.—In tabulating samples of band recoveries, I found that my own work was not entirely free of error. At the time I began my study at the Patuxent Research Refuge, the work of the banding office still suffered from the shortage of personnel brought on by the war. The process of coding and punching the IBM cards was far from complete. Some thirty or forty thousand cards, not yet filed, were in 12 different places in the office. No sample could be complete until these 12 places were examined. My wife took on the major task of reducing these 12 piles to 3, and of coding and punching cards for species which I was to analyze. A file of letters accompanying illegible bands was also processed and carded. A series of some 4500 incomplete cards was likewise reduced to about 3000. These cards bore recovery dates but lacked banding dates. They could not be further reduced in quantity without correspondence with a large number of banders who had failed to list the birds on their schedules. Some of the banders were now dead or no longer active. This material extended back to 1930; it seemed to include birds that were recovered before the banders sent in their reports. At least from the cards that my wife was able to complete, the bias from this source in my tabulations did not appear to be statistically significant.

A second source of minor error developed when I sorted the cards by machine. Even when International Business Machine Company

cards are correctly punched (and punching error averaged about 15 per thousand in the cards I used), the electric contact brushes on sorting machines are subject to inevitable wear. In the early stages of wear, an occasional card will be missorted as a result. I routinely thumbed through machine-sorted cards to catch errors in punching and to learn when the contact brush on the machine should be replaced. In compiling life tables for each species except mallards, I routinely sorted the cards twice.

A third source of error seemed to lie in my own assembling of usable recoveries. Reports of bands "found on a road" or "in the school yard" obviously are of little use in life-table work. I deemed it also advisable to discard reports of "skeleton found" and "remains found." (In small passerine species, these are unimportant; in pelicans they would tend to be a source of bias.) When specific methods of recoveries were being tabulated, reports giving "no information," "taken," "picked up," and "found" were also eliminated. All such discards in the white pelican amounted to 12.1 per cent of the cards on file. Together with conflicting or vague reports and birds found dead in colonies, they represented 20.2 per cent of the double-crested cormorant file. Since these eliminations were made without reference to date of recovery, I do not believe they introduced any new bias into the samples studied. Their removal, however, was often carried out by thumbing and visual inspection of each card. Some very thin cards tended to stick together so that in very large samples a small sorting error seemed to persist in spite of much precaution.

Variations in the manufacture of bands.--The bands placed on wild birds have varied considerably in design. Examples of those issued by the American Bird Banding Association during the second decade of this century were examined by me at the Patuxent Research Refuge. These are extremely thin bands and are not nearly as thick as those currently issued by the Fish and Wildlife Service. In my own experience with herring gull bands during the 1930's, when the manufacture of the bands was reasonably standardized, perceptible annual differences in the brittleness of the modern bands were also evident. More recently, Austin (1947a) has found tern bands much softer than usual and substitution necessary after two years. F. C. Lincoln (personal communication) informs me that variations in the composition of American bird bands have undoubtedly persisted since the program was taken over by the Federal Government; he believes that particularly fragile bands were used up to 1925. In nearly all cases I used this as the starting date for samples that I analyzed.

Environmental variations in wear.--The widely differing habits of the various families of birds subject bird bands to equally wide variations in wear. Severity of use theoretically progresses from air-dwelling species (swifts and swallows) and through the tree dwellers (vireos and kinglets), weed and grass dwellers (quails and pheasants), fresh-water swimmers (river ducks), and salt-water species (eiders and scoters). The severest use seems to be that associated with salt-water-feeding, rocky-ledge-nesting Alcidae and burrowing Procellariiformes (Lockley 1942, pp. 117-118).

According to Rohrman (1939), the resistance of aluminum to the atmosphere is "excellent," but halides and chlorides exert a dissolving action on the oxide film that ordinarily protects the surface of this metal; the rate of solution in distilled water is negligible. As far as I can determine we can expect salt-water birds to lose their bands at a faster rate than fresh-water birds, but the degree of difference between the two remains to be determined.

Most writers on avian longevity have not had to face the question of band durability. In the survival studies of small songbirds (Nice 1937; Lack 1943a, 1943b; Farner 1945), it seems to have no importance. Kortlandt (1942) concluded that it importantly distorted the mortality curve derived from the recovery of banded European cormorants. Marshall (1947) and Paynter (1947) seem to have overlooked this possibility in their analyses of longevity in the American herring gull.

In the United States, some veteran banders, who retrap large numbers of water birds over a period of years, frequently add a second band to the leg of an old bird wearing a fragile band put on some years before. O. L. Austin, E. W. Ehmann, and M. D. Pirnie might be mentioned in this connection. Dr. Austin systematically rebands 9-year-old common terns regardless of the condition of the original ring at that age (Austin 1942). When I began my study, A. S. Hawkins (in litt.) warned me to be cautious in interpreting waterfowl survival past the fifth year.

Loss of legibility.--While the loss of a bird band is a serious weakness in some retrapping programs, illegibility is as potentially serious in others that depend on the general public to report recoveries to a central office. A band with the name and address of the Fish and Wildlife Service missing obviously has very little chance of ever being reported. As to which occurs first--illegibility or band loss--I do not know; it may vary interspecifically.

In table 5 I have summarized the years of use on 147 illegible bands that the Fish and Wildlife Service had to etch with acid in 1946 and 1947. The results may approximate what takes place in nature, but the table is potentially biased by variations in the number of birds banded in previous years, and by the inclusion of bands mutilated by gunfire. I conclude that band loss or its equivalent is potentially a serious factor that must be constantly watched for in survival studies of adult birds. Its occurrence on a significant scale can often be detected by calculations of turnover and productivity. Its occurrence on a small scale is probably less easily perceived.

Table 5.—Onset of Illegibility in Bird Bands

This table summarizes the years of use represented by illegible bands that the Fish and Wildlife Service had to etch with acid in 1946 and 1947. The illegibility was generally brought about by the environment; some bands, however, had been mutilated by gunfire; others were mutilated in the act of being flattened out for mailing.

Species	Usual Band Size	Frequency by Years of Use													Total	
		1	2	3	4	5	6	7	8	9	10	11	12	13		
D.-c. Cormorant	3	-	-	1	-	-	-	1	-	-	-	-	-	-	2	
Canada Goose	8	-	-	-	1	-	-	-	-	-	-	-	-	-	1	
White Pelican	7	-	-	-	-	-	-	-	-	-	1	-	-	-	1	
Mallard	6	-	-	1	1	7	16	10	5	-	2	-	-	-	42	
Black Duck	6	-	1	-	5	5	8	2	4	-	1	1	-	-	27	
Pintail	6	-	-	-	1	5	7	11	6	4	3	3	5	-	45	
Canvas-back	6	-	-	-	-	-	-	1	-	-	-	-	-	-	1	
Ring-necked Duck	6	-	-	-	-	1	-	-	-	-	-	-	-	-	1	
Redhead	6	-	1	-	1	3	1	2	1	-	-	-	-	-	9	
Lesser Scaup	6	1	-	-	1	6	-	1	1	-	-	-	-	1	11	
Herring Gull	6	-	-	-	-	-	1	-	1	-	-	-	-	-	2	
Coot	6	-	-	-	-	-	1	-	-	-	-	-	-	-	1	
Gadwall	6	-	1	-	-	-	-	1	-	-	-	-	-	-	2	
Green-wgd. Teal	5	-	-	-	-	1	-	1	-	-	-	-	-	-	2	
TOTAL		1	3	2	10	27	34	27	20	6	6	5	5	-	1	147

Summary

At the present time, the difficulties of compiling accurate survival data for each stage of a bird's life encourage the synthetic construction of life tables based upon data obtained from diverse sources. Even when based on real conditions encountered in the field, survival statistics represent theoretical populations when means (averages) are computed. The survival of young birds after they leave the nest currently presents the greatest difficulty in the measurement of mortality. Contrary to recommendations by Lack (1946b) and Farner (1947), banding analyses of survival in the northern hemisphere should start not as of January 1 but as close to the fledgling period as the data permit.

Retrapping of adult birds tends to give minimal estimates of survival because of (1) individuals shifting their residence after nesting calamities (here estimated as 7 per cent of the song sparrows studied by Nice), or (2) homing failure, or (3) inefficiencies in the trapping technique. Under certain conditions correction factors for these sampling errors can be worked out.

The centralized banding files of the Fish and Wildlife Service, used in this study, were carefully scrutinized for weaknesses.

By checking all records as well as the banders, 146 discrepancies in each 1000 records were eliminated; an equal number of minor nature were found to be connected with dates of recovery. As used in this study, each 1000 banding records are thought to contain 2 questionable or spurious reports; undetectable errors in a mallard file were estimated at 0.5 per thousand.

Variations in the manufacture of bands and in usage by the birds make for band loss or illegibility that will potentially bias survival data. This bias is probably greatest in data for large birds in a marine environment.

Chapter III.—Characteristics of Avian Life Tables

Quality of primary data

The primary data in any life table may be regarded as the original information collected in the field. Even in the work on man, the quality of these may not be all that is desired. Census tabulations have been found, for instance, to show age-groupings favoring multiples of 5 or 10. They are also invariably deficient in giving the number alive in the first year of life (Hill 1936). These weaknesses are minor compared to the ones encountered in avian life-table work.

The striking defect in the quality of primary data available on bird populations lies in the absence of facts either on the numbers alive or on the numbers dying. The two sources of data have yet to be jointly available for work on the same population, although they are now separately available for a number of species. The defects in the quality of data arising from a retrapping program have been described in Chapter II. The quality of the mortality data may be examined here. Two questions regarding it are pertinent:

Is a banded sample of a bird population representative of the species? In some cases, the answer is yes; in others, no. Some species, like the small songbirds, are banded by hundreds or thousands throughout their breeding range. When nestlings are banded in this way, the life-table results may be fairly safely regarded as originating from a randomized sample of the species' population. In other species, the banded birds may all come from a single region or even a single colony. Life-table results in such circumstances should not be construed as holding for a continental population, although they may nonetheless be very valuable. Special problems may or may not be encountered when life-table results are based on trapped samples. Game species that in any way become conditioned to baited traps should be suspect in this connection, at least until better data are available. A great many water-fowl have, for instance, been banded by the U. S. Fish and Wildlife Service on its network of refuges throughout the country. At the present time, no one knows if these birds have better or poorer survival rates than nonrefuge birds banded at random as fledglings on scattered breeding grounds in Alaska and Canada. The survival-rate implications of a goose refuge, described by Elder (1946), might be mentioned in this connection. Another variable seems to present itself when we consider life-table results based on a short period of banding, in contrast to those arising from a banding program spread over many years. The former may give survival rates peculiar to an increasing or decreasing population; in the latter, the rates would tend to be more typical of a stable population (although this is not necessarily a safe assumption). Some of these variables will be encountered in the life tables constructed in Part II. Their overall effects may be small, but their presence should caution us to accept the results with reserve.

Is the mortality reported in a sample of banded birds similar in age distribution to unreported mortality in that sample? This question is no easier to answer than the preceding one. It may be rephrased in these terms: When a thousand black ducks are banded and only 150 are ultimately reported by the general public, are these 150 an unbiased subsample of the population? How can one be sure that the age distribution of the reported dead birds is similar to the age distribution of the 850 that never are reported? At the present time, we can say that the reliability of the subsample reported varies according to at least two factors. A gradually increasing rate of band loss will obviously mean that the reported mortality (or survival) is atypical of what is occurring among the birds that are unreported. The seriousness of this possibility in the large, salt-water birds has already been mentioned. At the present time, there is little published evidence that band loss occurs among the smaller passerine birds, many of which have been retrapped over long periods when wearing and weakness in the bands could easily have been noticed. (My wife and I have, however, seen a blue jay about to lose a very old band, and we have good reason to believe that it did so subsequently. We have also seen a male cardinal remove a band with its beak.) A second source of bias occurs when the method of recovery does not operate at all ages, or operates unevenly. This appears to occur especially where learning and experience coincide with age and reduce a bird's vulnerability to some mortality factor like hunting which is the source of the reports being studied. If mortality reports from other sources are few in number and little affected by this learning, reports of juveniles shot will exaggerate the proportion of mortality occurring in the first year of life. (This phenomenon will be demonstrated in table 13 later.) There are potentially at least two ways to discover this type of bias—(a) by productivity analyses and (b) by internal comparison of different methods of recovery.

Checks on bias

Productivity analyses.—Once a life table is constructed for the subadult and adult stages of the life span, ornithologists are sometimes in a position to calculate the total number of eggs the adults in such a table would normally have laid each year, how many young they normally would have hatched, and approximately how many fledglings on the average should have left their nests. It then becomes possible to estimate if the young produced by such a sample of adults will balance the mortality of the adults. This type of test enabled Lack (1943b) to recognize the bias introduced by gunning in life tables he set up for lesser black-backed and black-headed gulls; it also convinced Kortlandt (1942) that a serious loss of bands was occurring in his group of European cormorants. Lack (1943a, 1943b, 1946a) and Farner (1945) found no important bias in tables they constructed for passerine species.

Is this test crude or precise? The answer depends in part on the investigator's knowledge of the numerical trend in his population, the age at which the adults begin to breed, and the availability of satisfactory data on nesting success. As table 6 demonstrates, the

sensitivity of the test decreases when low mortality rates are encountered. Under conditions involving reasonably high rates of mortality, this test can probably be used to detect major bias in age distributions for species breeding at the end of one year. This really means that it is best used when one is working with small birds. In my own work, however, productivity analyses lost much of their potential effectiveness because so few facts are known about average productivity and the age at which the larger birds begin to breed.

Internal comparisons.--Up to the present, separate life tables have not been published for birds found dead, those shot, those killed accidentally, and so on. Accidental mortality seems like a singularly interesting type of sampling, but it is either poorly represented or poorly identified in banding recoveries.

Table 6.—Productivity Required to Keep a Population Level Stable

The species governed by this table must breed at the end of one year; the young produced are those alive at the start of the life table, here taken as some date such as September 1.

Adult Mortality Rate per Year	First-year Mortality Rate				
	70%	60%	50%	40%	30%
60%	4.0	3.0	2.4		
50%	3.4	2.5	2.0	1.67	
40%	2.7	2.0	1.6	1.3	1.14
30%	2.0	1.5	1.2	1.0	0.86
20%	1.3	1.0	0.8	0.67	0.57

Paynter (1947) has attempted to test the age bias in herring gull recoveries by first dividing the reports into two groups: "natural recoveries" (those birds found dead presumably from natural causes) and "artificial recoveries" (those in which man was the known agent of death or capture). The test then involved a comparison of the mean length of life of the birds in each sample. Although birds aged 0-1 comprised 46 per cent of the 674 "natural recoveries" and 60 per cent of the 578 "artificial recoveries," Paynter found an insignificant difference between the two means. He therefore concluded from this test that the two samples could be grouped together as the basis of an unbiased life table and that "those birds which died from human interference would in all probability have died at about the same time from natural causes."

I believe that Paynter's commendable pioneer effort failed for at least two reasons: (1) The mean is a measure of central tendency in a frequency distribution; it is not a statistic specific for a given age. Differences in data on the first year of life or the last years of life are therefore masked when mean

ages are compared.¹ (2) Statistical tests cannot be depended upon to detect unrandomized types of sampling; very often common sense will. Among Paynter's artificial recoveries, for instance, there were those from short-term retrapping operations carried out at the nesting colony by members of the Bowdoin Scientific Station. These could hardly be depended upon to record nonbreeding birds in the first two or three years of life. Scientific collecting and local gull-control work on this species likewise seem to me to be unrandomized types of sampling. Out of 44 herring gulls thus reported, only 3 were in their first year of life. Removal of the 44 from the "artificial" sample would change the percentage of first-year birds in it from 60.1 to 66.1 per cent.

Several statistical tests can be used to bring out differences in survival or mortality series based upon different methods of recovery, such as birds reported shot, found dead, captured by fishermen, and the like. In many cases, of course, the samples may be too small to demonstrate significant differences, and in any case a purely mathematical test can only yield a limited amount of information. It can, for instance, prove that the first of two sources of recovery could not be drawn from the same statistical universe as the second one, but it cannot prove which one is actually biased. Here one can see the overlap expected in the percentage of first-year birds found in two samples drawn from the same statistical universe. The probability that any two specific samples are significantly different in this respect can also be readily determined by a chi-square test. Computations of this type would show that the 46 per cent occurrence of first-year birds among Paynter's "natural recoveries" is significantly different from the 66 per cent occurrence in the "artificial recoveries" mentioned above. One or the other of these two sources is biased; a productivity analysis is still needed to indicate which one. Other statistical tests can similarly be used to test the difference between the slope of two life curves, but the investigator must still decide which curve coincides with the known productivity of the species.

Composite life tables for birds are only as reliable as the assumptions on which they are based. These assumptions, I am convinced, must be independently tested for each species or each group of species having similar habits. Mortality for waterfowl may, for instance, differ considerably from that reported for scavengers or raptore or songbirds.

¹Paynter's calculations of the mean length of life for both his samples were unfortunately carried out as if all his birds died at the conclusion of a year running from July 1 to June 30. A better approximation would be to assume that the recoveries were distributed around the midpoint of each year of life as Paynter did in calculating life expectancies in another part of his paper.

Before presenting a set of ornithological life tables in Part II of this report, it seems necessary that we further examine the mathematical weaknesses of both the dynamic and time-specific methods of analyzing mortality reports of banded birds. Although this examination is tedious in that it requires mental concentration on minute details, it will reward us by leading to a better understanding of analytical methods encountered in this type of research. The two important conditions to be noticed here are (1) constant and (2) fluctuating annual mortality rates.

Statistical treatment of constant mortality rates

If only one mortality factor is represented in the mortality reports, will this yield accurate data on the total annual mortality rate? This circumstance is closely approached in recovery reports of banded ducks and geese, where as many as 97 per cent of the recoveries may come from hunters. The actual percentage of a population taken by duck hunters is still unknown. Without attempting to guess even the approximate dynamics of such populations, let us assume that 60 per cent of the individuals alive on September 1 in species A are shot each fall, and that after the hunting season 25 per cent of the survivors are annually wiped out by accidents, diseases, and predation. The turnover in such a theoretical population is shown in table 7. In connection with this table, the following things should be noticed:

(a) By definition, mortality rate equals the number dying divided by the number exposed to the risk of dying. This latter value of course decreases with each death. In actuarial practice, the annual mortality rate is conventionally based on the number alive at the start of each year or age level. This compromise is crude but nevertheless inescapable. In the table under study, the 25 per cent mortality for disease, etc. was computed on the basis of the number exposed to this risk at the end of the hunting season; it actually represents only 10 per cent of the number alive at the start of the year.²

(b) In game species, the number of birds crippled and lost by hunters can reasonably be regarded as a more or less fixed percentage of the number shot. The inability of hunters to report the band number on

²When mortality factors operate at different but consecutive parts of a year, they affect the overall mortality rate as follows:

$$m_x = 1 - (1-m')(1-m'')(1-m''') \text{ etc.}$$

where m_x is the overall mortality rate for the year, m' , m'' , and m''' the mortality rates for specific factors operating at consecutive periods. If 3 factors (m_1 , m_2 , and m_3) operate contemporaneously, then

$$m_x = m_1 + m_2 + m_3 \text{ etc.}$$

Table 7.--Derivation of Overall Mortality Rate from a Single Nonfluctuating Source of Mortality Data

The important condition in this theoretical population is the constancy of each mortality factor. The table demonstrates how a sample of banded birds dying from one mortality factor will still yield a reliable estimate of the overall annual mortality rate due to all factors.

	Frequency by Age Intervals							Total
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	
THEORETICAL POPULATION								
(1) Alive at start	1000	300	90	27	8.10	2.43	0.73	1427.53 ^{3/}
(2) Shot (60%)	600	180	54	16.2	4.86	1.46		856.52
(3) Number left	400	120	36	10.8	3.24	0.97		571.01
(4) Diseases, etc. (25%)	100	30	9	2.7	0.81	0.24		142.75
(5) Number left	300	90	27	8.1	2.43	0.73		428.26
(6) Total losses	700	210	63	18.9	5.67	1.70		
(7) Annual Mort. rate	70	70	70	70	70	70		999.27
HUNTERS' SAMPLE								
A. <u>Dynamic Calculation</u>								
Number shot ^{1/}	600	180	54.0	16.20	4.86	1.46		856.52
"Alive at start"	856.52	256.52	76.52	22.52	6.52	1.46		1219.86
Mortality rate	70	70	70	70	77	100		
B. <u>Time-specific calculation</u>								
"Alive at start" ^{1/}	600	180	54.0	16.20	4.86	1.46		856.52
calculated deaths	420	126	37.8	11.34	3.40	1.46		600
Mortality rate	70	70	70	70	70	100		
DISEASE, ACCIDENT, AND PREDATION SAMPLE								
A. <u>Dynamic calculation</u>								
Found dead ^{2/}	100	30	9	2.7	0.81	0.24		142.75
"Alive at start"	142.75	42.75	12.75	3.75	1.05	0.24		203.29
Mortality rate	70	70	70	72	77	100		
B. <u>Time-specific calculation</u>								
"Alive at start" ^{2/}	100	30	9	2.7	0.81	0.24		142.75
Calculated deaths	70	21	6.3	1.89	0.57	0.24		100.00
Mortality rate	70	70	70	70	70	100		

1/ data from line (2) above

2/ data from line (4) above

3/ this column does not include any birds in age 6-7

cripples has no effect on the calculation of mortality rate so long as this inability is constant; it merely reduces the size of the sample available for study.

(c) The uncooperativeness of hunters who refuse to report the banded birds that they shoot likewise has no effect on the computation of mortality rate, but this uncooperativeness is here considered as being chronologically constant.

(d) Badly worn bands lacking the name of the Fish and Wildlife Service will obviously lower the number of older birds reported. This distortion will affect mortality-rate calculations for all ages in the dynamic method of analysis, but in the time-specific calculations it will affect only the later stages in the life table.

(e) In practice, birds are never reported and tabulated as fractions. Their deaths occur as discontinuous variables which inevitably produce some distortion in analyses. This distortion is minimized in the time-specific analysis where it is most noticeable in the later stages of the table. In the dynamic analysis, the distortion is carried forward into the earlier stages as well; it can be recognized as a pronounced tendency for the mortality rate to creep toward 100 per cent as one goes from year 0-1 to the end of the table.

Another hypothetical population is illustrated in figure 4. Here three successive mortality factors are at work: 10 per cent initially due to disease and accidents, 60 per cent of the survivors taken by hunting, 15 per cent of the remaining population dying from predation and other factors throughout the year. These three death curves all decrease at a rate of 69.4 per cent annually.

Can mortality and survival reports of banded birds be grouped together in constructing a life table? It should be obvious from table 7 that not only does each sample of mortality drop 70 per cent per year, but the various samples of living birds (those alive at the start of each year, those left at the end of the year) all decrease 70 per cent per year, too. Thus, if banding recoveries contain reports of birds dead as well as those alive in the same proportion year after year, these reports can be safely grouped in calculations of a constant mortality rate. The effects of combining such data are further shown in table 8.

Where mortality factors operate at constant levels, we cannot escape the conclusion that a time-specific analysis based on a single source of mortality may yield reliable estimates of the overall annual mortality rate. Since, under the same condition randomized samples of the living population likewise give the same result, they can be grouped with mortality data to form a survival series for calculations of mortality rate. Thus, the Dutch investigators--Kraak, Rinkel and Hoogerheide (1940) and L. Tinbergen (1946)--were justified in grouping together all types of recovery reports on banded birds into survival series and analyzing these on a time-specific basis. As far as I can determine, the recoveries that they used were random samples of bird populations reported by the general public to a central agency.

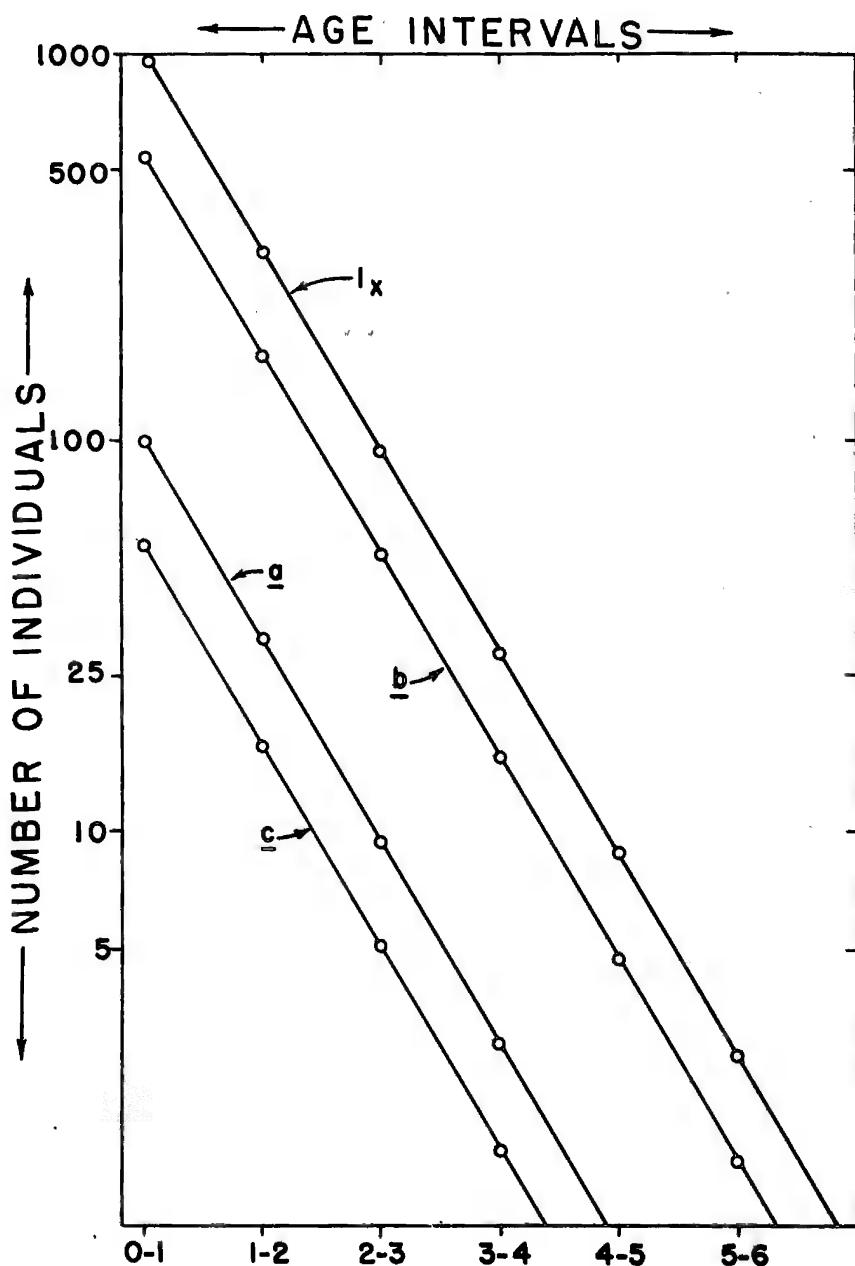


Figure 4.--Calculated changes in a theoretical population subject to 3 mortality factors which occur in the same order and at the same rate each year.

- l_x -- number of individuals alive at the start of each year
- a_x -- 10% mortality occurring before hunting season (disease, etc.)
- b -- the number shot each year (60%)
- c -- 15% mortality (disease, etc.) occurring after hunting season

Table 8.--Effect of Combining Mortality and Survival Data in a Single Life Table Involving Constant Mortality Factors

This table continues the study of the theoretical population in table 7. It is assumed that 10 per cent of the birds alive at the start of each year are recaptured and released, that one-half of the number shot are reported, that 5 per cent of the number left are retrapped, and that 1 per cent of the diseased birds are discovered each year. All recoveries are then grouped to form a life curve for a time-specific table and are used as a mortality curve in a dynamic table.

Sample	Frequency by Age Intervals						Total
	0-1	1-2	2-3	3-4	4-5	5-6	
Recaptured (10% of 1)	100	30	9	2.70	0.81	0.24	142.75
Shot (50% of 2)	300	90	27	8.10	2.43	0.73	428.26
Retrapped (5% of 3)	20	6	1.8	0.54	0.16	0.05	28.55
Found dead (10% of 4)	10	3	0.9	0.27	0.08	0.02	14.27
Total	430	129	38.7	11.61	3.48	1.04	

TIME-SPECIFIC LIFE TABLE

Alive at start	430	129	38.7	11.61	3.48	1.04
Deaths	301	90.3	27.09	8.13	2.44	1.04
Mortality rate	70	70	70	70	70	100

DYNAMIC LIFE TABLE

Deaths	430	129	38.7	11.61	3.48	1.04
Alive at start	613.83	183.83	54.83	16.13	4.52	1.04
Mortality rate	70	70	71	72	77	100

When birds are retrapped by a single bander or a research station, however, the survival reports thus obtained do not necessarily involve a random sampling of the age distribution in a bird population. Time-specific analyses of common terns retrapped on Cape Cod and reported by the Austins (1932, 1938, 1942) contain an additional variable which is examined in a later section.

Statistical treatment of fluctuating mortality rates

Are dynamic and time-specific analyses reliable when the overall mortality rate is fluctuating from one year to another? That a fluctuation does exist between the first- and second-year mortality rates of many birds has long been surmised by ornithologists. As early as 1926, Whittle and Whittle attempted to measure the difference for purple finches, but the homing responses of young and adult birds have usually frustrated attempts to analyze retrapping data along these lines. In more recent years, Lack (1943a, 1943b, 1946a, 1946b) has successfully used mortality reports in centralized banding files to demonstrate the degree of this fluctuation in a number of British birds; Buss (1946) has reported a similar condition in winter-trapped ring-necked pheasants; and more extensive fluctuations have been described for European cormorants

(Kortlandt 1942) and herring gulls (Marshall 1947; Paynter 1947).

Time-specific analyses.--Our original question may be approached by examining the turnover data in another hypothetical population outlined in table 9. Under these exaggerated circumstances, the time-specific analysis of mortality data breaks down completely. Its use in ornithological literature appears to have been based on the following reasoning:

(a) Survival rate equals the number alive at the start of one year divided by the number alive at the start of the previous year. $s_x = \frac{l_2}{l_1}$

(b) The numerator and denominator of this fraction can both be multiplied by the mortality rate without changing the equation. $s_x = \frac{l_2 q_x}{l_1 q_x}$

(c) But the number alive at the start of each year times the mortality rate equals the number dying that year; $d_2 = l_2 q_x$ and $d_1 = l_1 q_x$

(d) Therefore, survival rate can be found by simply dividing the deaths of one year by the number of deaths in the preceding year. $s_x = \frac{d_2}{d_1}$

Table 9.—Dynamic Versus Time-specific Computations in a Theoretical Population. Based on the use of mortality data only

Age Interval	Population		Dynamic Life Table		Time-specific Life Table	
	Number Alive at Start	Number Found Dead	Mortality Rate	Survival Rate	Mortality Rate	Survival Rate
	0-1	1000	250	25%	75%	0
1-2	750	250	33%	67%	0	100%
2-3	500	250	50%	50%	0	100%
3-4	250	250	100%	0	0	100%

The weakness in this line of thought of course lies in the fact that the mortality rate may differ from one year to another. Hence in step (b) above, instead of being able to use q_x in both numerator and denominator, only q_1 and q_2 are available. In the consideration of constant mortality rates in table 7, the time-specific method stood up well because both mortality rates q_1 and q_2 equaled 70 per cent. In table 9 these mortality rates equaled 25 and 33 per cent respectively. The time-specific table broke down as a result.

Buss (1946, pp. 76-77) has divided the number of birds shot in two successive years to show survival of game-farm ring-necked pheasants released in various states. His results almost certainly are not survival rates and are subject to correction. Because $\frac{d_2}{d_1}$ equals survival

rate only under one condition, I have termed this ratio survival index in this report and represented it by s_i in algebraic notations. Despite its variability, the index is not a useless statistic. It can be used with caution, and a few of its characteristics are worthy of notice here:

(a) If the survival rate in a dynamic calculation fluctuates from one year to another, the survival-index value obtained in a time-specific computation will fluctuate much more violently. This is evident in time-specific computations used in table 1 where all the birds were reported shot. Another illustration based on birds reported found dead is given in table 10.

Table 10.—Dynamic Versus Time-specific Computations in a Composite Life Table for Herring Gulls

Actual Sample	Dynamic Life Table from Marshall (1947)				Time-specific Life Table (explored here)			
	Age Interval ¹	Number Dying	"Alive at Start"	No. Deaths	Mort. Rate ²	"Alive at Start"	No. Deaths	Mort. Rate ²
0-1	2298	3806	2298	60.4	2298	1729	75.2	
1-2	569	1508	569	37.7	569	295	51.8	
2-3	274	939	274	29.2	274	83	30.3	

1/ in years

2/ per cent per annum

(b) Any given value for survival index in a time-specific analysis may be the result of a wide combination of mortality rates (q_1 and q_2) in the dynamic part of a composite life table. For instance, a survival index of 20 will result, if, in the dynamic analysis, the successive mortality rates are 80 per cent and 80 per cent, 75 and 60 per cent, 60 and 30 per cent, 50 and 30 per cent, and so on. Two of the combinations just cited are illustrated in table 11.

Table 11.—Vagaries of Survival Index Calculations

Year	Alive at Start	No. of Deaths	Mortality Rate	Survival Rate	Survival Index
1	1000	750	75%	25%	20%
2	250	150	60%	40%	20%
3	100	30	30%	70%	

$$\text{Here } s_i = \frac{d_2}{d_1} = \frac{150}{750} = 20\% \text{ and } \frac{d_2}{d_1} = \frac{30}{150} = 20\%$$

Table 12 further illustrates some of the combinations possible.

(c) It should be noticed that certain combinations of decreasing dynamic mortality rates can result in constant values for

survival index. That the decreases need not be abrupt may be seen in figure 5. Here successive mortality rates (per cent per annum) were set up as 39.34, 38.91, 38.21, 37.11, 35.41, 32.89, 29.41, 25, 20, 15, 10.59, etc.³ The resulting survival index is 60 per cent for 15 con-

Table 12.--Values of Survival Index for $\frac{d_2}{d_1} \times 100$

d_1 and d_2 = deaths in two successive years; s_1 and s_2 = survival rates same periods; q_1 and q_2 = corresponding mortality rates.

s_2	s_1									q_2
	10	20	30	40	50	60	70	80	90	
10	10.0	22.5	38.6	60.0	90.0	135	210	360	810	90
20	8.9	20.0	34.3	53.3	80.0	120	187	320	720	80
30	7.8	17.5	30.0	46.7	70.0	105	163	280	630	70
40	6.7	15.0	25.7	40.0	60.0	90	140	240	540	60
50	5.6	12.5	21.4	33.3	50.0	75	117	200	450	50
60	4.4	10.0	17.1	26.7	40.0	60	93.3	160	360	40
70	3.3	7.5	12.9	20.0	30.0	45	70.0	120	270	30
80	2.2	5.0	8.6	13.3	20.0	30	46.7	80	180	20
90	1.1	2.5	4.3	6.7	10.0	15	23.3	40	90	10
	90	80	70	60	50	40	30	20	10	
					q_1					

secutive age intervals. While this result is identical to a time-specific survival rate (= survival index in the sense of this paper) reported for the lapwing by Kraak, Rinkel, and Hoogerheide (1940), it seems to me improbable that such a peculiar set of statistics will be frequently found to cover such a long span of time. The situation should be watched for in shorter periods of observation.

Dynamic life-table analyses.--In table 13, I have set up another hypothetical population in an effort to explore the difference between dynamic and time-specific analyses. Here three sets of mortality sources are identified as occurring in consecutive order each year. One source represents a fluctuating factor: 65 per cent of the first-year birds alive at the start of a hunting season are shot; at subsequent age intervals, only 50 per cent are shot. Under the conditions of this hypothesis, several additional facts about these methods emerge:

(a) In populations with a fluctuating mortality factor confined to one part of the year, sampling time importantly affects

³The successive mortality rates (q_2) can be found by starting with a given mortality rate for the first year (q_1) and developing a series with the formula

$$q_1 = \frac{q_2}{s_1 + q_2}$$

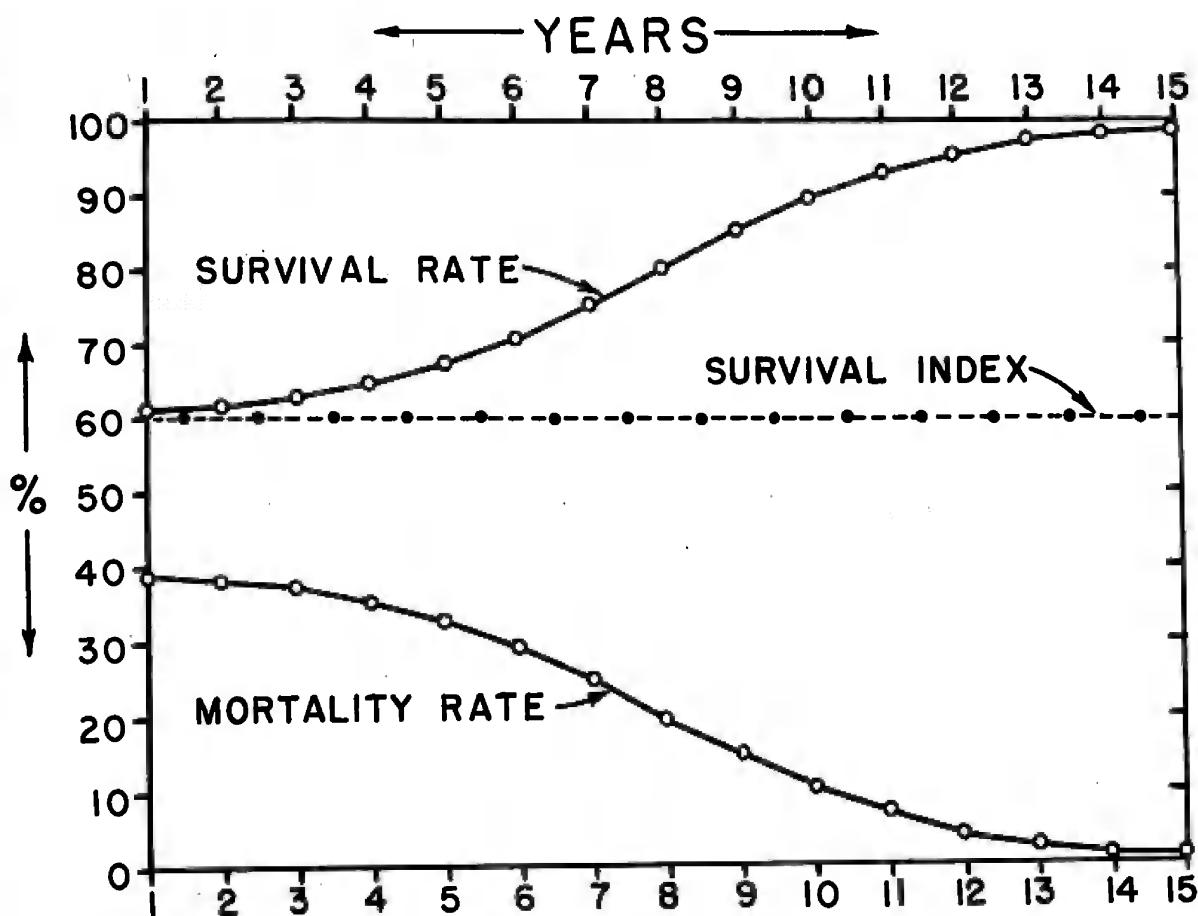


Figure 5.—A Theoretical Example of a Constant Series of Values for Survival Index Accompanied by a Progressively Increasing Survival Rate in the Population.

the results:

(1) Samples taken earliest in the year give the most accurate basis for mortality-rate calculations.

(2) Samples taken after the operation of the fluctuating factor fail entirely to demonstrate its presence.

(b) The time-specific method satisfactorily duplicates the overall mortality rate when it is used on the early-season sample but it tends to exaggerate the fluctuation when it is used on the hunting-season sample; the dynamic method gives only an approximation of the fluctuation in both situations.

Table 13.—Derivation of Overall Mortality Rate When One Factor is Fluctuating

This a comparison of dynamic and time-specific methods in analyses of a theoretical population with a fluctuation in the mortality rate and the sampling segregated according to different mortality factors.

Age Intervals in Years	0-1	1-2	2-3	3-4	4-5	5-6	6-7
THEORETICAL POPULATION							
Number alive at start	1000	266	101	38	15	6	2
5% dead (disease, etc.)	50	13	5	2	1	0.3	0.1
Alive start of hunting	950	253	96	36	14	5 ¹ /	2
65% then 50% shot ²	618	126	48	18	7	3 ¹ /	1
Alive end of hunting season	332	126 ¹ /	48	18	7	3 ¹ /	1
20% then lost (disease, etc.)	66	25	10	4	1	1	0.2
Surviving end of year	266	101	38	15 ¹ /	6	2	1
Total dead in year	734	165	63	24	9	3	1
OVERALL MORTALITY RATE	73.4	62	62	62	62.1	62.1	61.9

MORTALITY RATES CALCULATED FOR COMPOSITE LIFE TABLES BASED ON SAMPLES

Initial disease sample							
Dynamic method	70.0	62.2	62.5	63.3	65.8	73.7	100
Time-specific method	73.4	62.0	62.0	62.0	61.7	64.3	100
Hunting sample only							
Dynamic method	75.2	62.2	62.5	63.3	65.7	72.5	100
Time-specific method	79.5	62.0	62.0	62.0	62.1	62.0	100
Subsequent disease, etc.							
Dynamic method	62.1	62.2	62.5	63.3	65.6	72.6	100
Time-specific method	62.0	62.0	62.0	61.9	61.9	62.3	100

¹/ the entire table was computed to 2 decimal places; rounding off the numbers has left slight discrepancies, which are apparent in the final results.

²/ 65 per cent of those alive at the start of the hunting season are shot in age interval 0-1; in subsequent years, 50 per cent are shot

One additional point of contrast between the dynamic and time-specific methods should be mentioned here. When samples available for study are small, the dynamic method of calculation always helpfully increases the number of variates (here birds alive) available for study; at the same time, the time-specific method decreases the number dying each year. If the samples are very small, the time-specific method may be useless. This will be illustrated by many examples in subsequent chapters.

The effect of whole numbers on mortality-rate calculations

If a mortality rate is absolutely constant from one year to another, it is obvious that this would require the postulation of fractional values at the lower end of a mortality series. With a mortality rate of 50 per cent per year, a population of 100 should die off as 50, 25, 12.5, etc. in successive years. Because 12.5 birds cannot die off in real life, a constant rate of mortality can be easily distorted in small samples. In bird-banding analyses, this distortion appears in both dynamic and time-specific calculations. (Statistical workers will recognize that both are derived from frequency distributions of discontinuous variates.) In dynamic calculations, the distortion is greatest at the latter end of the mortality series, but Lack's method of calculating "birds alive at the start of each year" tends to carry the distortion into the early years as well. This is illustrated in table 14. Mortality rates calculated by the time-specific

Table 14.--Distortion in Mortality Rate Produced by Failure to Obtain Report of the Last Death in a Hypothetical Mortality Series

Mortality rate is here calculated by the dynamic life-table method. It is assumed that every dead bird is recovered but the last one (marked by asterisk). In nature where only a fraction of banded birds are recovered, and where mortality must be recorded in discontinuous (nonfractional) numbers, this situation is commonly approached.

Age	Actually Alive in Population at Start of Year	Number Dying during year	Calculated Number Alive at Start of Year	Calculated Mor- tality Rate per Year (%)
0-1	1024	512	1023	50.05
1-2	512	256	511	50.10
2-3	256	128	255	50.20
3-4	128	64	127	50.39
4-5	64	32	63	50.79
5-6	32	16	31	51.61
6-7	16	8	15	53.33
7-8	8	4	7	57.14
8-9	4	2	3	66.67
9-10	2	1	1	100.00
10-11	1	(1)*		

life-table method would, in table 14, yield exactly 50 per cent for all ten years except the last age interval. This method is, of course, also affected by the discontinuity of whole numbers, but the early mortality rates are not statistically dependent on later mortality reports near the end of the mortality curve.

In dynamic calculations of mortality rate, the distortion caused by whole numbers at the end of a mortality curve may be formulated as follows:

$$d_s = 100 \left(\frac{1}{l_a} - \frac{1}{l_a+m} \right) d_a$$

where

d_s = net amount of distortion in the mortality rate expressed as a per cent,

d_a = number of deaths reported for a given year a ,

l_a = number alive at start of that year, calculated by Lack's method, and

m = the missing mortality values at the end of the mortality curve.

Thus, in table 14 the distortion for year 5-6 is

$$\begin{aligned} d_s &= 100 \left(\frac{1}{31} - \frac{1}{31+1} \right) 16 \\ &= 100 (0.32258 - 0.31250) 16 \\ &\approx 1.61 \end{aligned}$$

In actual work with bird-banding data, the small size of the sample available at the end of a mortality series makes for obvious sampling errors which mask the statistical creep described here and preclude the possibility of calculating mortality rates for specific age intervals near the end of the life table. Under such circumstances, I have usually computed a mean annual mortality rate for these age intervals. As Part II will demonstrate, most of the samples are too small to yield valuable information on the later stages of a bird's life.

Adjusted survival series

When the number of banded birds recovered in a given period is expressed as a percentage of the total number originally banded, the result is called a recovery rate. The older banders, like Whittle and Whittle (1926), also called it a returning ratio—the value then referring to the percentage retrapped. Whittle (1929) was among the first to consider these annual percentages as an index of survival, but obvious trapping inefficiencies persuaded him and others against making refined calculations of annual mortality or survival rate. The best use of recovery rates appears to have been made by S. H. Low (1935), who used the trend in four years' retrapping data to conclude that a banded sample of mourning doves would shrink at zero at about the ninth year.

When the numbers of birds found dead or reported shot are expressed as year-by-year percentages of the cohort originally banded, the recovery series so constructed is every bit as real a mortality series (d_x) as the original raw data. The chief advantage of the conversion is that it permits recently banded birds to appear in the calculations for those age intervals where they were available for recovery. In composite life tables, the dynamic and time-specific methods of analysis still apply—and with the same variables discussed in this chapter.

Raw mortality data can similarly be expressed as the number recovered per 10,000 or 1000 banded and available for recovery in a given year or age interval. In an interesting life table for herring gulls, Paynter (1947) has attempted to utilize cohorts of recently banded birds by dividing the recoveries for each age by the number of years of recovery data available. This short cut is justified only in those rare cases where approximately the same numbers of birds are banded each year.

Summary

Avian life tables invariably lack primary data on either the number of birds surviving or dying. Even the field data gathered for one of these categories by banding samples may not always be typical of a species' population. Major sources of bias in life tables may be noticed when the results are checked by a productivity analysis, or when standard statistical tests are used to compare results obtained by two or more methods of recovery. When mortality rates are constant from one age to another, the overall mortality rate can be ascertained even though only one type of mortality provides all the band recovery data. Under such circumstances the results are not impaired by consistent crippling losses encountered (but not reported) by hunters or by the amalgamation of survival and mortality records into a single survival series in a time-specific analysis. When a mortality factor varies in degree from one year to another, the dynamic method of life-table analysis gives a better approximation of the overall mortality rate than the time-specific method does, especially if the banding recoveries precede or coincide with the operation of this factor (such as hunting) on the population. An alleged short cut for survival rate, obtained by dividing the deaths reported in one year by the deaths reported in the preceding year, is found to be statistically hazardous and is termed survival index in this paper. Expressing raw survival or mortality data as a percentage of the number of birds banded and available for study is recommended as a means of utilizing recent banding work in the construction of a life table.

These problems reduce themselves to these questions: Can banded birds reported as dead be properly regarded as raw material for a survival series? Are they examples of the living or examples of the dead? I conclude that in large randomized samples gathered

over many years (where adult mortality rates are reasonably constant), they may often be satisfactorily regarded as a sample of the living and thus analyzed on a time-specific basis. Where fluctuating mortality rates are encountered, especially in short-term investigations and small samples, such data must be used as mortality information in a dynamic life-table computation. The mortality rates thus derived from banding cohorts spread over a period of years should be reasonable approximations of average conditions affecting "theoretical" populations (in the sense of Chapter II). These are the type examined in Part II that follows. When "real" populations are similarly studied, as when a single cohort is used to provide mortality rates for specific years, wide annual fluctuations in a single mortality factor may take place. This particular condition will be encountered in Chapter XIV where the limitations of life-table calculations will be reconsidered.

Page 3

PART II
Explorations in Population Dynamics
of Representative North American Birds

In compiling avian life tables one is impressed with the scarcity of vital statistics for birds. While this perhaps is to be expected for the subadult and adult stages in each species, the lack of published quantitative information on productivity is astonishing. Many of these gaps in the literature can be promptly and easily filled, such as the mean number of young per nest in colonies annually frequented by banders; others will require more effort, like the determination of the percentage of unproductive females in a population or discovery of the age(s) at which certain species begin to breed. These are statistics needed for the ornithological handbooks of the future; their incompleteness or absence today may often mean that an abridged life table based on banding results cannot be either verified or expanded into a life table covering all the stages in the life history of a species.

The expository material in the following chapters is, for the most part, segregated under four headings for each species, Literature on Productivity and Survival, Banding Work in North America, Characteristics of the Sample Studied, and Abridged Life Tables. Commentary material has been generally divided under two headings, Age Ratios and Productivity and Population Dynamics. These two represent a discussion of the results and an attempt to integrate (where possible) the literature on productivity with the statistics obtained from abridged life tables. In the longer chapters, this breakdown of description and discussion is less clear cut. It is the purpose of Part II to present for biologists and conservationists survival and mortality statistics which, for the most part, can be used as yardsticks to assess the stability of bird populations.

Chapter IV.--Order Pelecaniformes (Family Phalacrocoracidae:
Cormorants)

Double-crested Cormorant

Literature on productivity and survival

The usual clutch of Phalacrocorax auritus is variously given by the older writers as 2-5 (Forbush 1925, p. 161), 3 or 4 (Bent 1922, p. 246), and 4-5 (Roberts 1932, p. 166), with sets up to 7 being reported (Dunlop 1915). On the Gulf of St. Lawrence, the great majority of double-crested cormorants are reported by Lewis (1929, p. 37) to possess a complete clutch of 4 eggs; Mendall (1936, p. 50) and Gross (1944, pp. 521-533) have reported on the number of eggs seen on visits to cormorant colonies in Maine (table 15). Mendall's summary (which does not give the number of nests actually seen) can be construed to represent a mean of 3.5 eggs per nest. Gross's census data yield a mean of 3.1. His Maine observations of course represent minimal estimates of full clutches. In this region, it therefore seems likely that the average clutch size is between 3 and 4; and in later computations this value will be kept in mind.

Table 15.--Double-crested Cormorant Clutches in the Literature

Size of Clutch	Lewis (1929), Gulf of St. Lawrence	Mendall (1936) Maine	Gross (1944), No. Seen	Maine Per Cent
1	-	-	201	8
2	-	8%	391	15
3	perhaps 5-10%	40%	1030	39
4	great majority	50%	954	37
5	very rare	2%	34	1
6	-	one record	-	-

The average number of eggs to hatch and young to fledge is yet to be calculated. Gross (1944) mentions 80 nests censused in Maine in which the average number of young was 2.2. This may be close to the probable number of young leaving the nest in that region. In the Netherlands, where European cormorants (Phalacrocorax carbo sinensis) are increasing at the rate of about 10 per cent per year, Kortlandt (1942) has calculated that 1.1 to 1.4 young fledge for each breeding female.

No survival studies of this species have been published. Kortlandt has intensively studied the age structure of the Netherlands population of the European cormorant. He concluded that mortality rates drop from about 36 per cent per year for birds in their first year of life after leaving the nest, to about 22 per cent for the second year, and about 16 per cent for the third year. For mature males it averaged 7-12 per cent per year, and for mature females 9-14

per cent. These extremely low adult mortality rates apparently offset the rather large number of nonbreeding birds which lower the reproductive potential of the population. This adult mortality rate has a constancy which remains to be determined; it would result in an exceedingly long turnover period for cohorts numbering 1000 or more birds. It is unfortunate that biologists unable to read Dutch cannot study Kortlandt's statistical treatment in detail.

By obtaining population counts over a period of years, by censusing banded birds in various colonies, and by analyzing recoveries of banded birds, Kortlandt also concluded that band losses due to rings bending open amount to about 10 per cent. This figure, which includes extra mortality caused by "accidents with the bands," is the first correction factor to have been offered for this type of bias in survival studies.

Banding work in North America

The relative success of double-crested cormorant banders in obtaining recoveries is illustrated in table 16. Among the 281 reports classified in this table as not used were 78 found dead during July or in cormorant colonies (nearly all of these the latter), 58 reported merely as "found," 37 with no data as to how obtained, 28 recorded as "probably shot," 25 "probably found dead," 24 vague as to how recovered, 15 skeletons or "remains," 7 with only the band and not the bird being found, 5 reported a year or more after actual recovery, 2 with conflicting dates, 1 with the species questionable, and 1 banding fatality.

Table 16.—Variations in Recovery Rates for Double-crested cormorants

Place of Banding	Bander	Dates of No. Banding	No. Banded	Recoveries	Effective Recovery Rate 1/	Total Recovery Rate 2/
				No. Used	Not Used	
East Coast						
Quebec	H. F. Lewis	1926-39	1076	74	11	6.9
Quebec	H. H. Southam	1937-41	2800	228	43	8.1
Maine	J. M. Cadbury	1938-41	2035	99	28	4.9
Maine	Miscellaneous	1935-40	282	19	5	6.7
Total		1926-41	6193	420	87	6.8
Inland						
S. D.	A. R. Lundquist	1929-37	1372	217	68	15.8
Sask.	F. G. Bard	1931-40	1928	268	87	13.9
Inland	Miscellaneous	1928-40	1529	208	39	13.6
Total		1928-40	4829	693	194	14.4

1/ this percentage is the number of recoveries used divided by the number banded; it is called the "effective recovery rate" in this paper

2/ this percentage covers both used and unused recoveries

The striking difference in recovery rates between the coastal (saltwater) birds and the inland birds at once raises the question of band loss, which will be taken up in a later section.

Birds banded after 1930 had not yet lived to age 14-15 at the time this study was undertaken. The small amount of banding work in the 1920's has created little opportunity for double-crested cormorants to be recorded at age intervals past 14-15. This in itself may create a small bias in life table analyses that follow.

Characteristics of the sample studied

The usable recovery reports of cormorants banded inland and on both coasts included 45 found sick or injured, 65 caught or captured, 128 known to have been caught by fisherman, 250 found dead, and 617 reported shot. These birds had been banded as young up through the nesting season of 1941. The monthly distribution of these shows frequency peaks for both October and April-May in the first year of life as well as in later years in the aggregate (figure 6). The same bimodal distribution holds for birds captured in various ways (figure 7), but the spring peak is not evident in birds reported shot.

A rough comparison of the various types of recovery, given in table 17, discloses that a significantly higher proportion of juvenile birds appears in the shot samples as compared to birds found dead, and that a parallel excess of juveniles occurs in coastal-banded birds found dead in contrast to inland juveniles found dead. The percentage of juvenile-mortality reports occurring from August 1 to November 30 is also significantly higher in the shot sample than in those reported found dead. There is thus a clear inference that shot samples are biased for age. The hypothesis that fresh-water birds retain bands longer than marine birds is not supported by the data on birds shot, but it does find confirmation in the data for birds found dead. Because 89 per cent of all the inland shot juveniles were reported from August 1 to November 30, it is possible that inland hunting pressure on young birds serves to mask the band-loss effect we are seeking in age ratios of this character. Annual variations in dates banded (inland versus coastal) further complicate this picture.

Composite life tables

Adult mortality rates.--If we may momentarily disregard the possible bias in reports of juvenile birds, we can examine adult mortality rates as calculated from reports on birds shot and found dead. Table 18 indicates that some inland-banded cormorants are now known to survive to at least their fifteenth year of life and that their adult mortality rate in this sample averaged about 22-26 per cent per annum. Similar data for marine-banded birds (table 19) give a maximum life span of only 7 years and a post-juvenile mortality rate averaging 39 per cent per annum. The discrepancy between the two survival curves is clearly seen in figure 8.

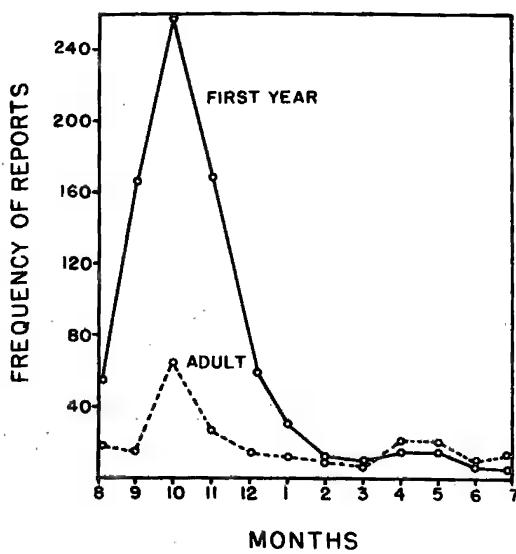


Figure 6

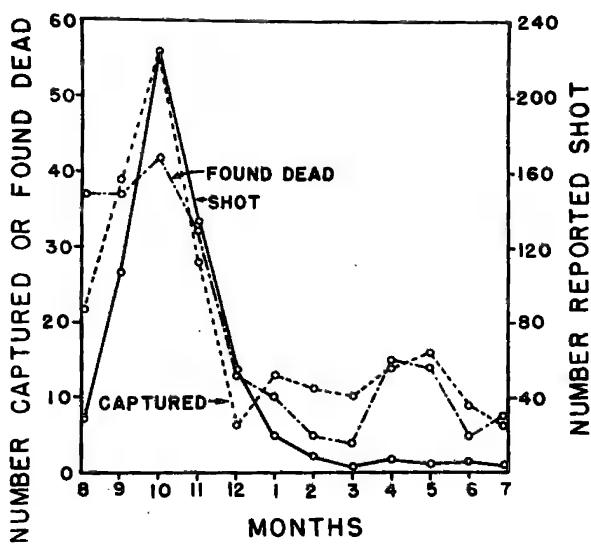


Figure 7

Figure 6.--The Frequency of Double-crested Cormorant Recoveries from (left) All Sources Classified According to Those Reported in the Birds' First Year of Life, and Those Reported Later.

Figure 7.--Monthly Distribution of Recoveries of Banded Double-crested (right) Cormorants. Among the 228 reported captured were 45 said to be sick or injured and 118 captured by fishermen.

Table 17.--Approximate Age Ratios in Double-crested Cormorants

These birds were banded as young through 1941; the ratios cover all usable reports received at Patuxent Research Refuge to August 31, 1946. "Juvenile" represents birds in their first year of life (August 1 to July 31). "Adult" in this table means all other birds past this first age interval.

(1) How Obtained	(2) Where Banded	(3) Juv.	(4) "Adult"	(5) Total	(3+5) % Juv.	(3+4) Juv./ Ad.	% Reported Aug. 1 - Nov. 30 Juv. Ad.
Shot	Inland	348	86	434	80	4.1	89 71
"	Coast	128	26	154	83	5.0	77 -
"	Total	476	112	588	81	4.2	86 64
Fd. dead	Inland	68	40	108	63	1.7	74 -
" "	Coast	93	21	114	82	4.4	70 -
" "	Total	161	61	222	73	2.6	71 57
Captured							
by fishermen		80	38	118	68	2.1	68 -
by misc. persons		85	25	110	77	3.4	85 -

* maximal values that will decrease when additional reports of the banded adults become available

No double-crested cormorant population with an age structure similar to that of these marine-banded birds could possibly maintain itself. We must conclude that the data in table 19 are biased. A close inspection of the two mortality curves in figure 8 reveals a gradually widening gap between the two. I infer that the increase in this gap principally represents band loss due to salt-water conditions. The small size of the samples possibly obscures the time when this loss begins. It would appear to be well underway during age 4-5 and (in this sample) complete by age 7-8.

As a check on the effect of band loss in life-table statistics, I recalculated table 18 using only the first 7 years of mortality data. This procedure yielded a first-year mortality rate of 79 per cent (cf. 80 per cent for the marine-banded birds) and a mean mortality rate of 71 per cent for all ages (cf. 66 per cent for marine birds). This agreement would appear to represent a type of experimental evidence that band loss is occurring among marine-banded cormorant populations. Band loss may occur among the fresh-water birds, too, but I was unable to appraise it at the time of this study.

The two mortality curves illustrated in figure 8 display minor peaks for age 5-6. There seems to be no possibility that these were caused by climatic conditions. One wonders if these are possibly

Table 18.--An abridged Life Table for Inland-banded Double-crested Cormorants--I

Based on birds banded as young in nesting colonies and later shot or reported as found dead. Each age interval starts August 1. The mortality series (d'_{x}) is the number recorded dead per 1000 banded birds available for study of each age interval.

(1)	(2)	(3)	(4)	(d_x)	(d'_{x})	(l'_{x})	(a_x)
Year	Number Banded	Age Class to be Studied ^{1/}	Banded	Number Recovered (by age class)	Mortality Series 1000 [$d_x \div (4)$]	Survival Series ^{2/}	Mortality Rate ^{3/}
1945	-	0-1	4829	450	93.2	123.9	75
1944	-	1-2	4829	58	12.0	30.7	39
1943	-	2-3	4829	21	4.3	18.7	23
1942	-	3-4	4829	11	2.3	14.4	
1941	44	4-5	4829	10	2.1	12.1	
1940	269	5-6	4785	14	2.9	10.0	
1939	391	6-7	4516	6	1.3	7.1	
1938	333	7-8	4125	4	1.0	5.8	
1937	198	8-9	3792	4	1.1	4.8	
1936	651	9-10	3594	2	0.6	3.7	
1935	406	10-11	2943	3	1.0	3.1	
1934	237	11-12	2537	0	0	2.1	
1933	259	12-13	2300	0	0	2.1	
1932	345	13-14	2041	3	1.5	2.1	
1931	579	14-15	1696	1	0.6	0.6	
1930	157	15-16	1117	0	0	0	
1929	764	16-17	960	0	0	0	
1928	196	17-18	196	0	0	0	
Total	4829	-	-	587	123.9	241.2	51
Mean Adult Rate (Years 1-2 to 14-15)-					30.7	117.3	26
Mean Adult Rate (years 2-3 to 14-15)-					18.7	86.6	22

1/ in years; birds banded in 1928 are available for all age intervals but represent the last year of banding available for reports of birds in age class 17-18

2/ the number alive at the start of each age interval; based on column d'_{x}

3/ per cent per annum; obtained from $d'_{x} \div l'_{x}$

associated with the age at which most of the birds in this species breed or first attempt to breed. This point can be re-examined in

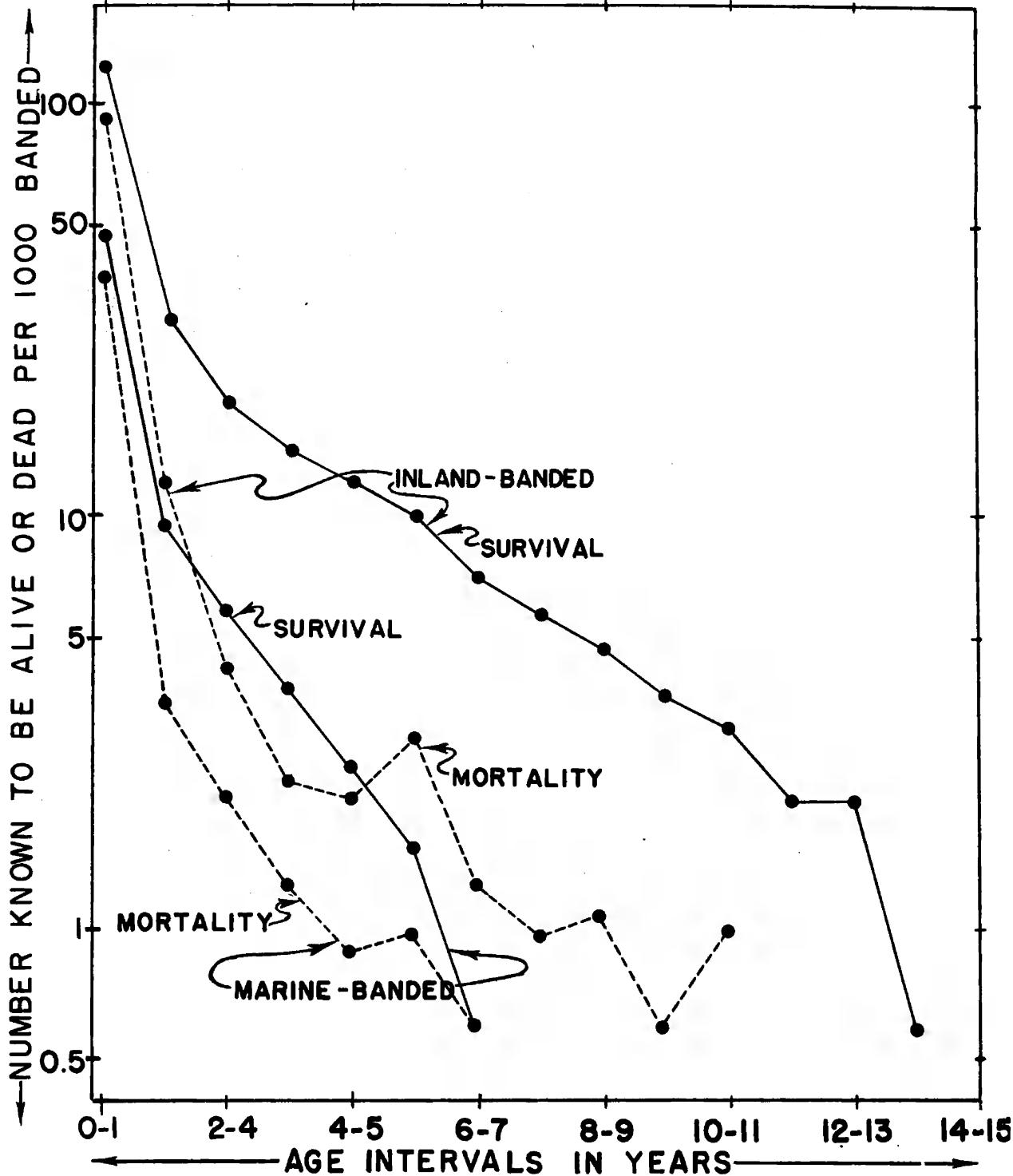


Figure 8.—Survival and Mortality Curves for Double-crested Cormorants Based on Reports of Birds Banded as Young and Later Shot or Found Dead.

Table 19.—An Abridged Life Table for Marine-banded Double-crested Cormorants

Based on young birds banded in nesting colonies and later reported shot and found dead. Each age interval starts as of August 1. The possible bias in this table is explained in the text. In addition to marine-banded birds shown in table 15, this table includes 42 birds banded in California and Oregon. Calculations for the 3 columns on the right are similar to those in table 18. Age intervals are in years; mortality rates are per cent per annum.

Year	Number Banded	Age Class Studied	Banded	Number Available	Recovered Birds (by age class)	(d_x)	(d'_x)	(l'_x)	(q_x)	Mortality Series		Survival Mortality Series	
										1000	$[d_x \div (l_x)]$	Series	Rate
1945	-	0-1	6235	239		38.3		47.8				80	
1944	-	1-2	6235	22		3.5		9.5					
1943	-	2-3	6235	13		2.1		6.0					
1942	-	3-4	6235	8		1.3		3.9					
1941	2320	4-5	6235	6		1.0		2.6					
1940	824	5-6	3915	4		1.0		1.6					
1939	633	6-7	3091	2		0.6		0.6					
1926-38	2458	7-8	2458	0		0		0					
Total	6235	-	-	294		47.8		72.0				66	
Totals and Means	(years 1-2 to 6-7)-					9.5		24.2				39	

a subsequent chapter on certain Laridae which exhibit a deferment of sexual maturity until at least the third year of life.

It should also be pointed out that, from the very start of each life table, marine cormorants are reported consistently less than fresh-water cormorants. I infer that this difference is principally due to the relative inaccessibility of dead birds once they are shot or die on the seacoast. The difference in recovery rates for the two groups, brought out in table 16, may primarily be due to the relative ease with which carcasses are recovered under fresh-water conditions and secondarily (at least at first) to band loss under salt-water conditions.

Juvenile mortality rates.—The potential bias in reports of juveniles shot may now be examined in table 18 by making a productivity analysis of the population implied by the survival series l'_x . Simple calculations show that if all the adults begin breeding at age 2-3 and all raise 2.5 young per pair to August 1, they will raise about 87 per cent of the young necessary to keep the population stable. I therefore feel that the presence of shot birds creates a bias in this life table, although it does not invalidate the comparison with an adult marine population recovered in a similar manner. There appears to be much less likelihood of this bias importantly affecting the mortality rate

for the second or for subsequent years of life. The mortality rate calculated here for the mature inland-banded cormorants may, however, be affected by band losses that exist even under fresh-water conditions.

A further examination of first-year mortality rate is carried out by constructing an abridged life table based on 116 birds found dead and 73 found sick or captured under various conditions (table 20). We now have three estimates of annual mortality rates for this species (table 21). If all the adults from age 2-3 breed and raise 2.5 young per pair to August 1 each year, the new sample population in table 20 will theoretically produce 45.6 young. At the present time, we have no factual basis to assume that all double-crested cormorants begin to breed at this age. The calculation of a first-year mortality rate for this species must for the present remain in doubt.

Table 20.--An Abridged Life Table for Inland-banded Double-crested Cormorants--II

Similar to table 18 but based on 73 birds found sick or captured by fishermen, and 116 reported as found dead. A few birds probably survived their capture. Age intervals start August 1 and are in years; mortality rates are per cent per annum.

(1)	(2)	d_x	d'_x	l'_x	q_x
Age Class to be Studied	Banded Birds Available (by age class)	Birds Recovered	Mortality Series 1000 $d_x \div (2)$	Survival Series	Mortality Rate
0-1	4829	131	27.1	39.6	68
1-2	4829	18	3.7	12.5	30
2-3	4829	3	0.6	8.8	
3-4	4829	8	1.7	8.2	
4-5	4829	5	1.0	6.5	
5-6	4785	12	2.5	5.5	
6-7	4516	5	1.1	3.0	24
7-8	4125	3	0.7	1.9	
8-9	3792	2	0.5	1.2	
9-10	3594	0		0.7	
10-11	2943	2	0.7	0.7	
Total	189		39.6	88.6	45

Table 21.--Estimates of Annual Mortality Rate in Double-crested Cormorants (expressed as per cent per annum)

Source of Reports Where banded	Shot + Found Dead		Found Dead + Captured Inland
	Marine	Inland	
Age Groups			
0-1	80	75	68
1-2	37	39	30
later	39	22	24

Population dynamics

The mortality rates for double-crested cormorants explored in this chapter are so considerably higher than those calculated for European cormorants by Kortlandt (1942) that one is tempted to regard the results as conflicting and contradictory. A simple analysis of the presently known population dynamics of the two species suggests consistency rather than contradiction within each species.

European cormorants, which have been reported to lay 4-6 eggs (Forbush 1925, p. 161), actually have an extremely low production of young in the Netherlands, Kortlandt finding only 1.25 ± 0.125 young per nest in his censuses and estimating 1.12-1.25 young per female as the number successfully fledged. The breeding potential is likewise lowered by delay in the onset of sexual maturity, the adult plumage not being attained until the birds are 3 years old (Forbush 1925, p. 158). It is at this age that most of the Netherlands birds of this species begin to breed; individuals, however, often do not nest until 2 years later (Kortlandt 1942, pp. 277-278). These adverse conditions are more than canceled out by the extremely low mortality apparently encountered. This is not only true of the subadult and adult years usually considered in abridged life tables but also of the short period immediately after the fledglings leave the nest.

On the other hand, Gross's (1944) census data from the Maine coast suggest that double-crested cormorants have a relatively high production of young. Lewis (1929, p. 58) has concluded that adult plumage (except for the crests) is acquired in 3 years. I would expect a slightly higher percentage of *auritus* to begin breeding at this age than of *carbo*, on the principle that larger birds tend to mature at later ages than do smaller birds; the actual difference between the two may, however, be relatively slight. The assumption of high production in the double-crested cormorants seems to be effectively counter-balanced by the relatively high mortality rates obtained in this study.

Summary

The picture here assembled is one of low production and low mortality rates in the European cormorant, high production and high mortality rates in the double-crested.

The mean clutch for double-crested cormorants, according to the literature, appears to be close to 4 in the Gulf of St. Lawrence and between 3.0 and 3.5 on the coast of Maine. Eighty nests censused by Gross (1944) had an average of 2.2 young. Mortality rates for young birds, once they leave the nest, are either unknown or require further study.

More than twice as many fresh-water-banded birds of this species were recovered as marine-banded, the difference being apparently due to the greater accessibility of carcasses inland and the greater

loss of bands through obliteration or disintegration under salt-water conditions.

Birds that survive the first year are subject to mortality rates of about 22-26 per cent, which apparently rise somewhat during the fifth year of life.

Chapter V.—Order Ciconiiformes (Family Ardeidae: Herons and Bitterns)

Black-crowned Night Heron

Literature on productivity and survival

The best quantitative nesting data on *Nycticorax nycticorax* is that reported from Massachusetts by Gross (1923). In 57 nests, the mean clutch was 3.2 eggs; in 199 other nests, there was a mean of 2.7 young. The mean number of young that fledge and leave the nest is not known. According to Bent (1926), the usual clutch is 3-5 eggs. Gross (1923) found birds in the first nuptial plumage active in nest building and incubating eggs; they also possessed fully matured gonads at that time.

Banding work in North America

The most extensive banding work on black-crowned night herons has been carried out in Massachusetts (277 recoveries of all kinds), with Michigan (67) next, followed by Colorado (38), New York (36), and Saskatchewan (33).

From 1926 to 1941 inclusive, 70 banders ringed about 10,767 birds of this species. By September 1, 1946, these birds were represented by about 308 usable recoveries, a recovery rate of 2.9 per cent. Among the unusable material were 105 reports (a) giving no information as to how obtained, or representing (b) birds found in heronries or as "remains," and (c) some that could not be verified against banders' schedules.

Characteristics of the sample studied

The migratory movements of night herons banded in Massachusetts have been mapped by Forbush (1925, p. xxiv) and by May (1929), who demonstrated a markedly random dispersal of the young birds in all directions. Lincoln (1936) and Cooke (1938) have listed 17 Latin American recoveries of U. S.-banded birds; 9 of these are reported in the first year of life, 2 in the second, 4 in the third, and 2 in the fourth. As far as I could determine, age variations in migratory habits do not introduce a bias into longevity analyses for this species.

In general, birds from Massachusetts west to South Dakota funnel toward Florida, Cuba, and the West Indies; those from California east to South Dakota and Nebraska move toward Mexico and Guatemala. The exact route taken by Illinois and Michigan birds to British Honduras is at present unknown.

The monthly distribution of reports of black-crowned night herons shot or reported as found dead is given in table 22.

First-year birds have a significantly higher number of reports than adults for the 4 months from August to November inclusive.

The difference in age ratios between birds found dead and those reported shot cannot be considered conclusive.

Table 22.--Monthly Variation in Recovery Dates Reported for Black-crowned Night Herons

Nestlings banded through 1941 and reported to 1946. Not shown here are 2 birds for which the month of recovery was uncertain, 4 killed by automobiles, 23 caught in mammal traps, and 57 caught sick, injured, or at fish hatcheries.

Month	(a)			(d)			(e)			(f)			Total in First Year	Total in Later Years
	Found Dead			Reported Shot										
	In 1st Yr.	In Later Years	Total	In 1st Yr.	In Later Years	Total	In 1st Yr.	In Later Years	Total	In 1st Yr.	In Later Years			
VII	(5) ^{1/}	-	(5) ^{1/}	-	-	-	-	-	-	(5) ^{1/}	-			
VIII	25	5	30	9	1	10	34					6		
IX	14	4	18	9	4	13	23					8		
X	18	3	21	19	4	23	37					7		
XI	12	2	14	13	3	16	25					5		
Subtotal	79%	41%	69%	78%	32%	61%	79%					37%		
XII	5	-	5	5	2	7	10					2		
I	4	3	7	3	2	5	7					5		
II	3	3	6	1	3	4	4					6		
III	2	1	3	1	2	3	3					3		
IV	1	5	6	-	4	4	1					9		
V	1	1	2	2	1	3	3					2		
VI	1	4	5	2	4	6	3					8		
VII	1	3	4	-	7	7	1					10		
Subtotal	21%	59%	31%	22%	58%	39%	21%					63%		
Total	87	34	121	64	37	101	151					71		
Age Ratio	72%	28%	100%	64%	37%	101%	68%					32%		

^{1/} a month or so after banding. In 2 cases the young birds had flown to another state. These 5 are not counted in the totals or percentages here.

Composite life tables

An abridged life table for night herons covers at least 13 years (table 23) and discloses an adult mortality rate of about 31 per cent per year compared to about 61 per cent for juveniles. These same data were also set up in another life table (not shown here) that yielded a mortality rate of 52 per cent between the first August 1 and December 31 and a mean rate of 30 per cent per annum for all years thereafter. This value of 30 per cent implies an adult mortality rate of about 2.5 per cent per month--a figure to which we will return shortly.

Table 23.—An Abridged Life Table for Black-crowned Night Herons

Based on nestlings banded from 1926 to 1934 inclusive. Age intervals are in years and start August 1.

Age Interval in Years	How Recovered (d _x)			Alive at Start of Year (l _x)	Mortality Rate Per Cent
	Found Dead	Reported Shot	Total Mortality		
0-1	42	44	86	141	61
1-2	5	8	13	55	
2-3	5	13	18	42	
3-4	4	1	5	24	
4-5	4	2	6	19	
5-6	1	4	5	13	31
6-7	1	1	2	8	
7-8	-	1	1	6	
8-9	-	1	1	5	
9-10	3	-	3	4	
10-11	-	-	-	1	
11-12	-	-	-	1	
12-13	1	-	1	1	
Total	66	75	141	320	44.7
Juv./Ad.	1.7	1.4	1.6	0.8	
% Juv.	64	59	61	44	

1/ mean for entire sample

Age ratios and productivity

If we bear in mind Gross's (1923) statistic of 2.7 young herons per nest, the bias in table 23 might be examined under several contingencies:

- (1) If all young herons of this species breed at the end of one year and each pair raises 1.6 young to August 1, the mortality rates of this table (23) would make for a stable population. The value of 1.6 potentially represents about 40 per cent mortality operating on the nestling average of 2.7 furnished by Gross. This mortality would have to occur between June or July and August 1—the start of the life table.
- (2) It seems to me wise to explore the assumption that all night herons begin to breed at 2 years of age. Under such conditions, table 23 would result in annual population decreases of about 10 per cent. While this situation probably did not prevail in the population from which this sample was taken, it is well to realize that the sample itself is small and there is a good possibility that some individuals might attain breeding condition at one year, and others only at 2 years of age.
- (3) Any tendency for (a) the older birds to lose their bands or (b) the deaths reported for first-year birds to be atypical of

unreported mortality at this level will obviously exaggerate the productivity required to keep such a life-table population stable. These tendencies may well enter the banding work here analyzed but the distortion they produce (if any) is unknown and seems to be a minor one in the sample studied.

On the evidence available at this writing, there is no hint that the banding data on survival are biased. The 40 per cent mortality mentioned above for nestlings seems to be too high to be acceptable. The alternative hypotheses are that not all female night herons are successful in raising young or that not all adults breed at the end of one year. There is a strong probability that this latter phenomenon governs the situation encountered here.

Population dynamics

Alexander (1944, 1945, 1946) has shown that an asymptote in the common heron population is rapidly regained following low densities induced by severe winters. Errington (1945, 1946) has also emphasized that such lows are followed by high rates of reproductive gain, and Elder (1945) has pointed out that this inveristy principle seems to be illustrated by the common heron. Although clutch size appears to be genetically fixed (Lack 1947), we can expect that the production of young will periodically vary in a given species. With only a single nesting study to furnish the important statistics on productivity in black-crowned night herons, and with only a small sample of banded birds to give us data on subadult and adult survival, no final picture of the population dynamics of this species can be given at this time.

The pieces of information available at the moment can, however, be fitted into an hypothesis, the outline of which is very instructive. The mosaic to be constructed requires information on the mortality suffered by young birds in the month after they leave the nest and on the percentage of unsuccessful and nonbreeding females. If about 52 per cent of the young die between August 1 and December 31, an estimate of 15 or 16 per cent mortality in July seems fairly conservative.

When a heron population with 2.7 young per successful female on July 1 is subject to juvenile mortality of about 16 per cent in July, and 2.5 per cent mortality for adults at the same time, the age ratios change as follows:

July 1	190 young per 70 successful females (2.7-1)
August 1	160 young per 68 successful females (2.4-1)

Now from table 23 we inferred that the ratio was 1.6 young for each female in the population, successful, unsuccessful, and

nonbreeding. It would therefore follow that on August 1 in our hypothetical population of herons we had 160 young per 100 females. Under these conditions, 32 females out of 100 were unsuccessful or nonbreeding. The turnover in this population follows the life table from this point: About 50 per cent of the young alive on August 1 die in the next 5 months; by July 31 additional young die equivalent to about 10 per cent of those alive on the preceding August 1. The surviving 40 per cent replace 30 per cent of the adults, and the population remains stable.

The following will perhaps clarify what would take place under such circumstances:

	<u>Population</u>	<u>Age Ratios</u>	
		<u>Alive</u>	<u>Dead</u>
Alive on August 1	160 young	200 adults	(0.8-1)
5-month mortality	80 young	20 adults	(4-1)
Alive on January 1	80 young	180 adults	(0.45-1)
7-month mortality	20 young	40 adults	(0.5-1)
Alive on July 31	60 yearlings	140 adults	(0.4-1)

When we say that 10 per cent of the young alive on August 1 die during the last 7 months of the year, this is the same as saying that 25 per cent of the young alive on January 1 die during this period. This is approximately the same mortality rate suffered by the adult birds ($40 \div 180 = 22$ per cent).

Summary

Banding studies of the black-crowned night heron in North America reveal it to be a highly migratory species, the eastern population (South Dakota to Massachusetts) moving south to Florida, Cuba, and the West Indies, the western population wintering in Mexico and Guatemala. Of 141 banded young alive on August 1, 52 per cent were later reported found dead or shot in the first 4 months. The mean adult mortality rate for the survivors was 30 per cent per year, the last bird in this sample dying in its thirteenth year of life.

A comparison of these data with the results of a nesting study by Gross (1923) carries no hint that the banding data are biased and suggests that about 30 per cent of the females one year of age or older were either unsuccessful or nonbreeding.

Chapter VI.—Order Anseriformes (Family Anatidae: Ducks, Geese, and Swans)

Mallard

Literature on productivity

Anas platyrhynchos apparently breeds at the end of one year. The most complete set of nesting statistics has been furnished by Girard (1941), who reported a mean clutch size of 7.13 eggs, 71.2 per cent of these hatching and about 4 young reaching the "flapper stage" (the age at which banding of the young often takes place). These data were acquired on refuges in western Montana where "diligent" predator control was exercised. Average clutch sizes elsewhere have been higher, usually around 8.5 (table 24). Nesting studies in Utah (Williams and Marshall 1938) and Montana (Girard 1941) each yielded 5.1 young per successful nest at the time of hatching.

Table 24.—Reproductive Success of North American Mallards—I

Where Studied Reference	B.C.	Alta-Sask. Cowan	Saskatchewan Kalmbach	Utah ^{1/} Furniss	Mont. Man. Lynch	Girard	Sowls	Totals and Means
	1948	1937	1938	1948	1941	1948		
Nests								
Number noted	19	188	33	-	-	-	36	276
Number hatched	9	105	25	-	-	-	12	151
% hatched	47	56	76	-	-	-	33	55 ^{2/}
Eggs								
Number noted	191	353 ^{3/}	265 ^{3/}	42	1582	1797	-	4230
Number nests	23	45	31	5	185	252	-	541
Mean clutch	8.3	7.8	8.6	8.4	(8.6) ^{3/}	7.1	-	7.82
Number hatched	76	-	-	-	953	1279 ^{3/}	-	2308
% hatched	63 ^{4/}	-	-	-	60	71.2	-	66 ^{5/}
Brood Size Hatched								
	-	-	-	-	5.1 ^{3/}	5.1 ^{3/}	-	5.1

1/ Williams and Marshall (1938)

2/ Kalmbach (1938) has reported 46.9 per cent and 62.2 per cent for nests in North Dakota in 2 successive years

3/ calculated from other statistics published by the authors

4/ based on 121 eggs in 19 nests

5/ for Utah and Montana data only (2232-3379=66 per cent)

Brood sizes have been reported by still other investigators, especially by Stoudt (1946) for Minnesota from 1937 to 1941 and by Fish and Wildlife Service biologists who carried out continental surveys in 1947 and 1948 (table 25). On the whole, these reflect much

higher reproductive success than the Utah and Montana studies, the average size brood being 7.17 for 1310 observations. No one familiar with the breeding grounds of waterfowl will doubt that the reproductive success of this group is subject to fluctuations. These hatching and brood data are not, I think, contradictory, but may be actually representative of typical variations encountered in the population dynamics of the mallard and other waterfowl.

Table 25.—Reproductive Success of North American Mallards—II

Where Studied	When Studied	Number of Broods	Total Number Young ^{1/}	Mean Number per Brood	References
British Columbia	-	84	509	6.0	Munro (1943)
British Columbia	1948	47	310	6.6	Munro (1948)
Alberta	1948	70	472	6.7	Smith (1948b)
Sask.-Alberta	1934-35	32	227	7.1	Kalmbach (1937)
Saskatchewan	1934-35	15	87	5.8	Furniss (1938)
Saskatchewan	1937	7	39	5.6	Furniss (1938)
Saskatchewan	1947	77	552	7.2	Lynch (1948)
Saskatchewan	1948	53	389	7.3	Soper (1948)
Manitoba	1947	65	403	6.2	Hawkins (1948)
Manitoba	1948	17	118	6.9	Hawkins & Cooch (1948)
North Dakota	1947	66	449	6.8	Hammond (1948)
North Dakota	1948	19	152	8.0	Stoudt & Davis (1948)
Minnesota	1937-48	758	5685	7.5	Stoudt (1948)
Total		1310	9392	7.1	

^{1/} calculated for the most part from other statistics in the original paper cited.

Recent attempts to gather data on the shrinkage in mallard brood size have not been very successful (table 26), although Stoudt's (1946, 1948) work in the Chippewa National Forest, Minn., seems to be a satisfactory appraisal of the early survival of young. This work covered a period when the continental waterfowl population was thought to be increasing. Much of it is a by-product of census work. While the data may be biased by field difficulties that prevent counts from being complete for the younger ducklings, it seems possible that the narrow time-span of the censuses also created a time-specific life-table effect: In other words, the size of the mallard clutch was gradually shrinking throughout the season. This means that the size of broods at hatching also decreased as the nesting season progressed. On a transect of the breeding grounds, the census taker would thus tend to record the early-hatched young in Classes II and III (table 26) and the recently hatched young from renestings in Class I. Excellent evidence for the progressive shrinkage in clutch size in other species has been given by Leopold (1933, p. 363), Errington and Hamerstrom (1937), Hamerstrom (1939), and J. B. Low (1945); and an important summary of the known data has been published by Lack (1947). Stoudt's

data indicate that, until the time they left their parents, young mallards suffered a mortality of about 20 per cent.

Table 26.--Reproductive Success of North American Mallards--III

Data classified (where possible) according to size of young in broods

Class Where Observed	I Downy Young			II 1/2 to 2/3 Grown			III About Ready to Fly		
	Number of Broods	Total Young	Mean No. per Brood	Number of Broods	Total Young	Mean No. per Brood	No. of Broods	Total Young	Mean No. per Brood
Alberta (Smith 1948)	33	231	7.0	28	186	6.6	9	55	6.1
Saskatchewan (Lynch 1948)	34	250	7.4	36	242	6.7	7	60	8.6
Saskatchewan (Soper 1948)	10	71 ^{1/}	7.1	23	156 ^{1/}	6.8	20	162 ^{1/}	8.1
No. Dakota (Hammond 1948)	28	192	6.9	29	175	6.0	9	76	8.4
No. Dakota (Stoudt and Davis 1948)	7	64 ^{1/}	9.1	5	38 ^{1/}	7.6	7	50 ^{1/}	7.1
Subtotal	112	808	7.2	121	797	6.6	52	403	7.8

Minnesota 1937-41 (Stoudt 1946)	110	880	8.0	227	1702	7.5	252	1764	7.0
1946 (Stoudt 1948)	8	62 ^{1/}	7.8	32	230 ^{1/}	7.2	27	189 ^{1/}	7.0
1948 (Stoudt and Davis 1948)	7	50 ^{1/}	7.1	43	328 ^{1/}	7.6	52	356 ^{1/}	6.8
Subtotal	125	992	7.9	302	2260	7.5	331	2309	7.0
Total	237	1800	7.6	423	3057	7.2	383	2712	7.1

^{1/} computed from other statistics furnished by the author

The age ratio at this early point in the cycle would appear to be about 7 young per successful female. The percentage of unsuccessful females in the population has yet to be ascertained. Some clues given by Kalmbach (1938) make a crude guess possible. Kalmbach divided the nesting season into halves and found that--for all species of ducks--nests in the first half were 57 per cent successful, those in the second half 79 per cent successful. He believed that these latter nests represented renesting attempts. If most of the 43 per cent of the hens (that failed the first time) actually renested, it would follow that

another 34 per cent of the hens (0.43 times 0.79) were also successful. This gives a total of 91 per cent. If only half of the 43 per cent renested, the total percentage of successful females would be 74 per cent. Using Kalmbach's statistics in this fashion (and they were not, of course, calculated solely for mallards), we can now see the range of age ratios possible at this stage of the life cycle:

	<u>Hypothesis</u>	<u>Data</u>
(1)	If no females renest, there will be about 2.3 juveniles per adult	$66 \text{ pr.} \times 7.0 = 462 \text{ young}$ $462:200 \text{ adults}::2.3:1$
(2)	If half renest, the ratio is 2.6 to 1	$57 \text{ pr.} \times 7.0 = 399 \text{ young}$ $23.5 \times 0.79 \times 7.0 = 130 \text{ young}$ $529:200::2.6:1$
(3)	If all unsuccessful the first time renest, then the age ratio is 3.2 to 1	$57 \times 7.0 = 399 \text{ young}$ $43 \times 0.79 \times 7.0 = 238 \text{ young}$ $637:200::3.2:1$

These estimates are minimal values because they do not consider mortality in the adults during the nesting period. If this were 25 per cent and we corrected (2) above by using 150 adults in lieu of 200 in the proportion, the age ratio in such a population would then be of the order of 3.5 juveniles to each adult. If it were 10 per cent, the age ratio would be 2.9. This review of some possible age ratios in mallards will, I hope, emphasize that high brood counts do not necessarily imply high ratios of young to adults in mallard populations. An enormous fund of information on age ratios in this species has been accumulated during the hunting season, but a critical analysis of these data has not yet been published.

The sex ratio for adult and subadult mallards appears to be close to an even one. McIlhenny (1940) has reported trapping 1728 males and 1713 females from 1934 to 1938 in Louisiana where the birds winter. Ratios approaching this one have also been directly observed by Beer (1945) in southwestern Washington and by Erickson (1943) in Minnesota. Mallards having an unbalanced sex ratio (61.3 per cent males to 38.7 per cent females in a sample of 9783) have been trapped in northeastern Illinois from 1940 to 1945 (Mann, Thompson, and Jedlicka 1947); but trapping data in that state seem to be biased (Hawkins, personal communication). The preponderance of males sometimes noted in hunters' bags may not be significant (Hawkins, Bellrose, and Smith 1946).

Banding work in North America

Since 1924, about 275,000 mallards have been banded in North America, mostly in subadult or adult stages, and usually during the hunting season (September to January or February). Critically competent age determinations have been used by relatively few banders after September 1 in any given year. The most notable banding operations carried out in this connection have been the work of the Game

Division of the Illinois State Natural History Survey under the direction of A. S. Hawkins, and the work of John Jedlicka for the Forest Preserve District of Cook County, Ill. A report on the former is in process of preparation (Bellrose in litt.); a mimeographed report on the latter has been written by Mann, Thompson, and Jedlicka (1947).

The 40,000 mallard recoveries in the files of the U. S. Fish and Wildlife Service represent an enormous research opportunity that may not be fully utilized for years to come. While I found the usefulness of the recoveries severely restricted by the unknown age of most of the birds and the statistically awkward dates of banding (i.e., during the hunting season), I was certainly impressed with the cursory nature of my own analyses of mallard recoveries and the great amount of unpublished information still remaining in these files.

The mallard banding work, as of 1946, was particularly unrepresentative of young birds banded in the best breeding range before the start of the hunting season. The two most notable geographic gaps, in terms of banding stations, were Alaska and Texas.

Banded literature on survival

At the time this study was undertaken, no detailed survival studies of wild-trapped mallards in North America had been published. An important report by Bellrose and Chase (1950) on the survival of Illinois mallards appeared after this chapter was written; it will be discussed in Part III of this report. Munro (1943) has given the age distribution of 3387 British Columbian birds banded from 1928 to 1940 and later recovered up to January 31, 1943; the oldest individual had at least reached age interval 10-11.

Höhn (1948) analyzed the mortality reported for the European race of this species (Anas p. platyrhynchos). Banding reports on 305 adult-banded birds gave a mean annual mortality rate of 65 per cent, and a mean after lifetime of 1 year and 2 months. For 828 birds ringed as young (67 per cent of which were known to be hand-reared), "89% died during the first year, 9.6% during the second year, 0.6% during the third year and 0.8% during succeeding years. The average period of survival was 4.5 months after ringing." Höhn points out that these results were based almost entirely on shooting, and that—while it cannot be assumed that the banded always recorded the hand-reared status of young birds—there is no a priori reason to assume a difference in survival between hand-reared and wild-reared mallards.

Considering the ease with which imprinting is reported to occur in waterfowl (Lorenz 1937), it seems to me that it would be more conservative to assume that—until facts are available—some hand-reared waterfowl will adopt human beings as "social companions" and become unduly vulnerable to hunting as a result. A re-examination of Höhn's data is therefore pertinent. From table 27, in which the first age interval starts as of the date of banding, it is evident that no difference exists in first-year mortality rates, but the

known-hand-reared birds have a significantly higher adult rate of mortality than the wild-reared birds. Although the 271 birds in the latter sample may contain some hand-reared individuals, their mean adult mortality rate, 58 per cent, is of the same order as that (65 per cent) for 305 birds reported by Höhn (1948) as banded as adults. Some difference, therefore, does exist between wild-reared and hand-reared birds but this in itself demands an explanation of the similar rates computed for the first year of life.

Table 27.—Mortality Reported for Mallards Banded in Great Britain
(after Höhn 1948)

Age Interval in Years	Reported as Wild-reared				Hand-reared Birds			
	Rept. as Dead	Alive at Start	Annual Mortality Rate % Per Year	Rept. as Dead	Alive at Start	Annual Mortality Rate % Per Year		
0-1	239	271	88	497	557	89		
1-2	20	32	†	60	60	100		
2-3	5	12	58	0	0	-		
3-4	3	7	†	0	0	-		
4-5	4	4	†	0	0	-		

According to Höhn (in litt.), mallards may hatch in England from early April to early August, the juveniles in his samples being banded from May to August (the majority during the latter month). He also estimates (in litt.) that the young were ringed when approximately 2-3 months old. Since the British wildfowling season opens in August 1, one is tempted to conclude that the vulnerability of all young birds to the gun is so great that even wild-reared young face a tremendous disadvantage in Great Britain. Such a situation almost implies that the 65 per cent mortality rate for adults reported by Höhn is in itself unusually high by North American standards. With an adult mortality rate of this order and a theoretical first-year mortality rate of 75 per cent, all British mallards would have to raise at least 5.2 young per pair to the "flapper" stage (date of ringing). This productivity may be compared to the average of about 4 per successful female reported by Girard (1941) for conditions involving diligent predator control in western Montana and 7 young (nearly ready to fly) per successful female observed by Stoudt (1946) in Minnesota. The actual age ratio in mallard populations is certainly much less than the values per successful female. Crude estimates of second-nest possibilities, carried out in an earlier section, suggest to me that the high degree of reproductive success necessary to maintain the British mallard population is within the limits of reproductive efficiency in this species. Girard's data indicate, however, that this level of efficiency is not always attained in North America even when diligent predator control is exercised.

Characteristics of the samples studied

About 85 per cent of the mallard recoveries in North America occur during the hunting season. It is thus very difficult to test the selective bias of the shot samples for age groups. The varied history of North American waterfowl in the past 25 years also suggests that a host of different factors have affected the survival of mallards. Three of these are well known: the great drought of the 1930's, changes in hunting regulations, and a marked increase in hunting pressure. They imply that a mallard life table may vary from decade to decade and from one part of the country to another. This possibility will be explored in Chapter XIV. In general, the recoveries tend to have a monthly peak in November. Birds affected with botulism at the time of banding were excluded from all the analyses that follow for this species.

Survival of birds banded as young

Wild-reared birds.--The samples of wild-reared juvenile-banded mallards used in this study do not include any birds known or even suspected to be hand-reared. This culling out severely reduced what originally seemed to be a statistically satisfactory sample. In a preliminary review, I found that in a sample of 81 birds banded as juveniles in Utah 87 per cent were shot in their first year of life in contrast to 68 per cent for 133 banded at random elsewhere on the continent. This randomized sample (table 28) represented birds banded about as follows: in Alaska (2), British Columbia (4), Alberta (29), Saskatchewan (15), Manitoba (15), Michigan (11), Wisconsin (3), Minnesota (2), North Dakota (18), South Dakota (17), Nebraska (2), Washington (10), and Oregon (5). It yielded a first-year mortality rate of 68 per cent and a mean adult mortality rate of 50 per cent per year. With the Utah bandings added, these would become 73 and 52 per cent.

Table 28.--Mortality Reported for Mallards Banded as Juveniles in North America

All birds banded prior to September 1; Utah bandings excluded.

Age Interval in Years	Wild-reared (banded through 1939)			Hand-reared (banded through 1938)		
	Reported Shot	Alive at Start	Mortality Rate (%)	Reported Shot	Alive at Start	Mortality Rate (%)
0-1	111	163	68	368	448	82
1-2	26	52	—	56	80	70
2-3	13	26	—	16	24	—
3-4	8	13	—	1	8	—
4-5	1	5	50	3	7	—
5-6	1	4	—	2	4	49
6-7	3	3	—	0	2	—
7-8	0	0	—	1	2	—
8-9				0	1	—
9-10				(1) ^{1/}	1	—
Total Adults	52	103	50	80	129	62

^{1/} data for this age interval were technically incomplete at the time this table was compiled in the fall of 1947

A breakdown of the recoveries using bandings through 1941 disclosed no difference in survival between 142 juveniles banded in Alaska and Canada and 128 banded in the northern part of the United States. A group of 86 males appeared to have a higher mean mortality rate than 75 females but the difference was not statistically significant.

Hand-reared birds.—Samples of hand-reared birds were examined in passing. Among these, the percentage shot during the first year of life did not vary with the month of banding (June, July, or August). It did, however, markedly differ from that for wild-reared birds. Preliminary data also indicate that the adult survival rate of wild birds may not be attained by these hand-reared individuals until the third year of life (table 28). By this time, however, only 5 per cent of those reported are still alive. It is difficult to appraise the bias in the mortality curves thus constructed for game-farm birds. The birds that I examined were released from California to Delaware and as far north as Alberta and Manitoba. Errington and Albert (1936) have analyzed in detail one release in Iowa; similar analyses for other releases would undoubtedly be instructive. The sample studied in table 28 included not only birds raised on game farms but a small number reared from wild eggs by the Delta Waterfowl Research Station. The latter appeared to possess the migratory behavior of wild-reared individuals; they also represented nearly half of the 24 hand-reared individuals known to be alive at the start of the third year of life.

Survival of adult birds

Hunters' reports.--A reasonable approximation of an adult mortality rate can be obtained by analyses of reports for birds that were unaged at the time of banding. If the mortality reports for the first year are discarded in such a series, the remaining reports refer to adults, the ages being $x + 1$, $x + 2$, and so on. A sample of this type is illustrated in table 29. To form it, I used 181 recoveries accumulated by F. C. Lincoln for birds he banded in Illinois in 1922, 228 more of Lincoln's for Illinois birds banded in 1926, and 821 banded in Missouri by L. V. Walton and John Brocker from 1922 to 1928. This Mississippi Valley subsample, which included some nonhunting reports, had a mean mortality rate of 46.5 per cent per annum. Although many of these birds were banded in years when bands may not have been very durable, I failed to detect any important evidence of band loss. (This would show up as abnormally high mortality rates during the early ages in the life table.) A second subsample consisted of 1762 males banded mostly by A. J. Butler in British Columbia and by G. M. Benson and his associates at Malheur National Wildlife Refuge in Oregon; these birds were found to have a mean adult mortality rate of 48.5 per cent. A few more mortality reports in the Pacific coast sample can probably be expected. These should total less than 0.2 per cent of the total and should not appreciably affect the mortality rates calculated. Evidence against the existence of differential mortality rates for male and female mallards is given in Chapter XIV.

Table 29.—Mortality in Adult North American Mallards That Were Unaged When Banded

Each age starts as of September 1; game-farm birds and those suffering from botulism when trapped were excluded. Not all the records included here could be checked against the banders' original reports. The Pacific coast birds were all males; x means additional reports can be expected.

Where Banded..... When Banded..... Age Interval (Yrs)	Mortality			Total Number Dead	Alive at Start Each Age	Mortality Rate (per cent per annum)
	Mo. - Ill.	Pac.	Coast			
	1922-28	1926-35				
x + 1 to x + 2	578	949		1527	2992	51.0
x + 2 to x + 3	333	376		709	1465	48.4
x + 3 to x + 4	135	170		305	756	40
x + 4 to x + 5	74	110		184	451	41
x + 5 to x + 6	50	66		116	267	43
x + 6 to x + 7	26	42		68	151	45
x + 7 to x + 8	14	17		31	83	
x + 8 to x + 9	11	15		26	52	
x + 9 to x + 10	5	7		12	26	
x + 10 to x + 11	3	6		9	14	
x + 11 to x + 12	0	4		4	5	45
x + 12 to x + 13	0	x		(0)	1	
x + 13 to x + 14	0	x		(0)	1	
x + 14 to x + 15	0	x		(0)	1	
x + 15 to x + 16	1	x		(1)	1	
Total	1230	1762		2992	6266	—
Mean Mort. Rate	46.5%	48.5%		—	—	47.7

The mean of 47.7 per cent is among the first approximations (Bellrose and Chase 1950; Hanson and Smith 1950) we have for a waterfowl's adult mortality rate on this continent. The sample covers a period during the 1930's when ducks were decreasing in North America. Drought in itself might not affect the adult mortality rate of such mobile animals, but the tightening up of hunting regulations (which paralleled the drought) presumably would. Further analysis of such factors is pursued in Part III of this study.

Mammal-trappers' reports.—For about every 100 hunters reporting, one mammal trapper has caught a banded mallard in traps usually set for muskrats. Unless some mallard behavior trait associated with age influences this phenomenon, banding samples so gathered are a pertinent check on survival calculated from hunting mortality. The data are not specific for age and the samples very small, but they should reflect approximately correct rates of annual survival in adults. I found that the dates of capture by fur trappers ran from August to April (inclusive), with a major frequency peak in November and a minor peak in March. About two-thirds of the reports came from Canada; the rest were spread over 24 states in the United

States. Major fluctuations in the frequency of muskrat trapping presumably affect the number of banding recoveries, but I did not attempt to detect them in the small sample available for study.

The breakdown for a sample of 92 mallards banded through the spring of 1937 is illustrated in table 30. Eighty-nine of these had a mean annual mortality of 50 per cent from age $x + 1$ to age $x + 7$ inclusive, the data for subsequent age intervals being slightly incomplete. The survival curve is fairly straight on semilog paper for 6 or 7 years. A possible increase in survival rate in the later years of a mallard's life (when vulnerability to predation and hunting possibility decreases with added experience) is studied in Chapter XIV.

Table 30.—Banded Mallards Reported Caught In Mammal Traps

These birds were unaged at the time of banding (August to April inclusive). Each year starts as of June 1, but all birds recovered in the same year in which they were banded (age interval x) are omitted. Brackets and the symbol X signify age intervals that were not included in the totals and means at the bottom of the table because the data for these ages were incomplete or unavailable when this table was compiled.

When Banded Symbol	1922-37		1922-41	
	I_x	d_x	I_x	d_x
Age Interval in Years	Caught in Traps	Calculated Mortality	Caught in Traps	Calculated Mortality
$x + 1$ to $x + 2$	46	28	89	54
$x + 2$ to $x + 3$	18	7	35	15
$x + 3$ to $x + 4$	11	4	20	5
$x + 4$ to $x + 5$	7	3	15	X
$x + 5$ to $x + 6$	4	2	X	X
$x + 6$ to $x + 7$	2	1	X	X
$x + 7$ to $x + 8$	1	-1	X	X
$x + 8$ to $x + 9$	2	(1)	X	X
$x + 9$ to $x + 10$	(1)	(1)	X	X
Total	89 ^{1/}	44 ^{1/}	114 ^{2/}	74 ^{2/}
Mean Mortality Rate (per cent per year)	50		51	

1/ excludes last 2 age intervals

2/ for first 3 age intervals only

A second sample, banded up through the spring of 1941, greatly increases the amount of recoveries available for 4 age groups and gives a 3-year mean mortality rate of 51 per cent.

Age ratios and productivity

From our short review of the nesting biology of the North American mallard, it is evident that no precise analysis of average

productivity per adult is possible at this time. Allowing for 10 per cent adult mortality during the nesting season and renesting by 50 per cent of the females that lose their first clutches, reproduction would appear to result in an age ratio of the order of 3 juveniles per adult at the time of banding. Even with considerable juvenile mortality between the flapper or banding stage and the peak of the hunting season, this productivity would be ample to stabilize the population implied in tables 28, 29, and 30. First-year mortality rates of 68 or 73 per cent as of September 1 are thus possible, but being derived from small samples they must await further verification. Discussion of the dynamics of mallard populations is deferred until Part III, where variations in mallard mortality rate are given in greater detail.

Summary

The literature on North American mallards reveals that the mean clutch for 541 nests observed was 7.8 eggs, that the mean number of young in 1310 broods was 7.1, and that the shrinkage in brood size for 758 broods in Minnesota was about 20 per cent from hatching to the time the young were ready to fly. The number of unproductive or unsuccessful females in the population is still unknown, but 55 to 70 per cent of all nests studied have hatched.

Preliminary calculations of first-year mortality rates for a small sample of 163 wild-reared juveniles yielded 68 per cent, the bias in this figure being difficult to assess. A mean adult mortality rate of 47.8 per cent for 2992 birds unaged at the time of banding checked fairly well with a smaller sample of birds of known age. Birds captured in mammal traps had the same overall mortality rate as those reported by hunters. Hand-reared birds had a considerably higher initial mortality rate than wild-reared ones, the difference possibly persisting until the third year of life. The mortality rates found here for North American birds were considerably lower than those reported for mallards in Great Britain.

Literature on productivity and survival

Aythya americana is one of the few ducks on which a quantitative nesting study has been published. During 1938-40 in Iowa, J. B. Low (1945) found that clutches averaged 9.8 eggs, that 45 per cent of these eggs produced young, and that approximately 70 per cent of the young reached the start of their first fall migration. Signs of fall migration were evident as early as August 20.

Banding work in North America

The principal banding work on redheads has been carried out in Utah's Bear River marshes by Fish and Wildlife Service personnel: A. V. Hull, F. C. Lincoln, Alexander Wetmore, and G. E. Musbach, whose 460 recoveries of juvenile-banded birds made up the bulk of life-table data available for this study. Wetmore's pioneer work in 1915 and 1916 was not used in my compilations, because of the uncertain permanency of the bands.

Characteristics of the sample studied

The migratory distribution of juvenile Utah-banded birds has been mapped by Williams (1944), who also demonstrated that most of the Bear River Redheads reported shot by hunters are actually killed in their first autumn. This latter phenomenon is so striking that a monthly distribution of the hunters' reports is given in table 31 where about 12 per cent of the dates consist of approximations made by banding clerks. Of the juvenile birds reported shot in their first autumn, 78 per cent were apparently killed in September and October. This is impressively higher than a value of 46 per cent that I similarly calculated for 457 juvenile mallards. A parallel segregation of adults reported shot in the first 6 weeks of the season (=61 per cent) may be contrasted to 33 per cent for a small sample of adult mallards. Since it would appear that these redheads were markedly more sensitive to hunting pressure than mallards, a comparison of mortality curves of the two species becomes particularly interesting.

Williams (1944) has clearly shown that the Utah-raised redheads winter principally in the Salton Sea area of southern California and on the lower coast of Texas. Lincoln's (1939) postulation of a migration route from Bear River to Chesapeake Bay unquestionably has some bias, but--as Robbins (1949) has shown--the annual magnitude of this phenomenon is almost negligible.

The dual wintering grounds of redheads raised in the prairie provinces are demonstrated in table 32. This particular unit of the redhead population was banded mostly by personnel of Ducks Unlimited (Canada) since 1939 and occupies a minor role in the life tables that follow.

Table 31.—Monthly Distribution of Hunters' Reports of Redheads Raised in Utah

Banded in Utah 1926-33. About 12 per cent of these recovery dates represent approximations made by banding clerks at the time reports were received in Washington.

Where Reported Shot	Usual Hunting Season	Months in Which Birds Were Reported Shot											
		Shot as Juveniles					Shot as Adults						
		Sept.	Oct.	Nov.	Dec.	Jan.	Total	Sept.	Oct.	Nov.	Dec.		
Alta.	IX/15-XII/14	-	-	-	-	-	-	-	1	-	1	-	2
Sask.	IX/15-XII/31	-	1	-	-	-	1	1	-	-	-	-	1
Mont.	IX/16-XII/31	5	4	-	-	-	9	-	1	-	-	-	1
N. D.	" "	1	1	-	-	-	2	-	2	-	-	-	2
Minn.	" "	1	2	-	-	-	3	1	2	-	-	-	3
Mich.	" "	-	-	1	-	-	1	-	-	1	-	-	1
Wyo.	" "	18	16	1	-	-	35	1	1	1	-	-	3
S. D.	" "	3	-	-	-	-	3	2	-	1	-	-	3
Neb.	" "	6	-	-	-	-	6	1	4	1	-	-	6
Colo.	" "	20	26	1	-	-	47	1	7	1	-	-	9
Kan.	" "	-	2	-	-	-	2	-	1	-	-	-	1
Nev.	" "	8	8	2	1	-	19	2	3	-	1	-	6
Wash.	X/1-I/15	-	-	-	-	-	-	-	1	-	-	-	1
Idaho	" "	-	12	2	2	-	16	2	-	-	-	-	2
Ore.	" "	-	1	1	-	-	2	-	-	1	-	-	1
Utah	" "	-	153	11	2	-	166	3	-	2	-	-	5
Calif.	" "	-	17	8	5	4	34	5	8	5	1	1	19
Ariz.	X/16-I/31	-	2	4	-	-	6	3	-	-	-	-	3
N. M.	" "	-	5	1	-	1	7	4	-	-	-	-	4
Okla.	" "	-	1	2	-	-	3	2	2	-	-	-	4
Tex.	" "	-	5	22	6	5	38	3	5	-	-	-	8
La.	XI/1-I/31	-	-	-	-	-	-	-	-	1	-	-	1
Md.	" "	-	-	-	-	-	-	-	-	1	-	-	1
Mexico	-	-	2	2	1	1	6	-	1	-	-	-	1
Total		62	257	58	18	11	406	9	44	22	12	1	88
Per cent		15	63	14	4	3	99	10	51	25	14	1	101

Composite life tables

Mortality statistics on this species are complicated by the extreme vulnerability of new-flying late-hatched young to shooting (Hochbaum 1944, p. 142). The extraordinary age ratio of 1 adult to 23 juveniles found in hunters' bags at Delta, Manitoba, by Hochbaum (1944, p. 133) is exceeded by the ratio of 1 adult to 33 juveniles for the banded birds shot in Utah (table 31). These two sources of data are not, of course, exactly comparable. Cecil S. Williams, who has had abundant field experience on the Bear River Migratory Bird Refuge, emphasizes in a letter (May 12, 1947) that differential sex migrations occur also in Utah, that adult female redheads tend to desert their

Table 32.—Monthly Distribution of Hunters' Reports of Redheads Raised in Canada

Banded before September 1 as young birds in Manitoba and Saskatchewan by Ducks Unlimited (Canada). About 12 per cent of the recovery dates represent approximations made by banding clerks at the time reports were received in Washington.

Where Reported	Shot	Shot as Juveniles					Shot as Adults					
		Sept.	Oct.	Nov.	Dec.	Jan.	Total	Sept.	Oct.	Nov.	Dec.	Jan.
Alta.	-	1	-	-	-	-	1	-	-	-	-	-
Sask.	1	1	-	-	-	-	2	-	-	-	-	-
Man.	12	10	1	-	-	-	23	2	4	2	-	8
Ont.	1	3	2	-	-	-	6	1	1	-	-	2
<u>Subtotal</u>	<u>14</u>	<u>15</u>	<u>3</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>32</u>	<u>3</u>	<u>5</u>	<u>2</u>	<u>-</u>	<u>10</u>
N. D.	1	-	1	-	-	-	2	-	1	-	-	1
S.D.	-	-	-	-	-	-	-	1	2	1	-	4
Minn.	3	11	3	-	-	-	17	1	4	3	-	8
Wis.	1	4	-	-	-	-	5	-	1	1	-	2
Mich.	-	5	5	-	-	-	10	1	8	6	-	15
<u>Subtotal</u>	<u>-</u>	<u>5</u>	<u>20</u>	<u>9</u>	<u>-</u>	<u>-</u>	<u>34</u>	<u>3</u>	<u>16</u>	<u>11</u>	<u>-</u>	<u>30</u>
Neb.	-	-	-	-	-	-	-	2	1	-	-	3
Kan.	-	-	-	-	-	-	-	-	-	1	-	1
Mo.	-	-	-	-	-	-	-	1	1	-	-	2
Ill.	-	-	-	-	-	-	-	-	1	1	-	2
<u>Subtotal</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>-</u>	<u>4</u>	<u>4</u>	<u>4</u>	<u>-</u>	<u>8</u>
N.Y.	-	2	1	-	-	-	3	-	-	-	-	-
Pa.	1	-	-	-	-	-	1	-	-	-	-	-
Md.	-	1	1	1	1	-	3	-	-	1	7	3
Va.	-	1	1	-	-	-	2	1	-	3	1	5
N.C.	-	-	2	-	-	-	2	-	-	-	2	2
<u>Subtotal</u>	<u>-</u>	<u>1</u>	<u>4</u>	<u>5</u>	<u>1</u>	<u>-</u>	<u>11</u>	<u>1</u>	<u>-</u>	<u>1</u>	<u>10</u>	<u>6</u>
OKLa.	1	2	1	-	-	-	4	-	-	-	-	-
Tex.	-	8	1	1	10	-	-	-	5	1	3	9
La.	-	-	2	-	-	-	2	-	-	1	-	1
Miss.	-	2	-	-	-	-	2	-	-	-	-	-
Ala.	-	-	1	-	-	-	1	-	-	-	-	-
<u>Subtotal</u>	<u>-</u>	<u>1</u>	<u>12</u>	<u>5</u>	<u>1</u>	<u>-</u>	<u>19</u>	<u>-</u>	<u>5</u>	<u>2</u>	<u>3</u>	<u>10</u>
<u>Total</u>	<u>19</u>	<u>37</u>	<u>32</u>	<u>10</u>	<u>2</u>	<u>100</u>	<u>7</u>	<u>25</u>	<u>23</u>	<u>12</u>	<u>9</u>	<u>76</u>
<u>Per Cent</u>	<u>19</u>	<u>37</u>	<u>32</u>	<u>10</u>	<u>2</u>	<u>100</u>	<u>9</u>	<u>33</u>	<u>30</u>	<u>16</u>	<u>12</u>	<u>100</u>

young more readily than do any other species, and that on their breeding grounds juvenile redheads--without the association of experienced wary adults--tend to be brought to bag more readily than other ducks.

The similarity of these field appraisals from different parts of the continent strongly suggests that a redhead life table based almost entirely on hunters' reports will contain an undue proportion of birds in their first year of life.

An abridged dynamic life table for 471 redheads (table 33, part A) indicates that the life span was short for most of the population (less than 5 full years for 99 per cent of the birds sampled) and that the adult mortality rate was of the order of 54 per cent. In an effort to confirm this adult rate, a time-specific life table (table 33, part B) was also constructed, using banding work up to 1942. The small number of adult recoveries encountered was disappointing, but a reasonably close approximation of the same rate was obtained. The juvenile mortality rates derived here will be examined under Age Ratios and Productivity.

Age ratios and productivity

The preponderance of juvenile birds (87 per cent) in table 33, part A, is identical to that found by Williams (1944) in an analysis of 357 recoveries of Utah-banded birds. The data would at first seem indicative of band loss in the adults, but Hochbaum (1944) has shown that 92 per cent of 277 redheads bagged at Delta, Manitoba, were first-year birds. The banding data thus reflect a condition found in the field and are not biased by a loss of bands among the older birds.

If we consider the age ratio among the birds alive in table 33, part A, we obtain a value of 4.2 juveniles per adult as of September 1, equivalent to 8.4 young per pair. J. B. Low (1945) found that the average at hatching in Iowa was 4.4 young per pair, and I conclude from his paper that the age ratio in Iowa is of the order of 1.5 to 1.8 young per adult at the start of migration. This discrepancy between the life-table population and a natural population arises here from the violation of a basic assumption in life-table compilation: that the birds reported as dying in each age interval are typical of the unreported or unrecovered birds dying in similar age intervals. There is a strong probability that after the close of the hunting season first-year birds die from natural causes at approximately the same rate as adult birds. Now, if the juveniles are, say, twice as vulnerable to hunting as adults are and if hunting reports form the sole basis for the life table, the life table would not be typical of mortality occurring after the hunting season. First-year mortality rates would then be exaggerated. This type of exaggeration has been illustrated in table 13 in Chapter III. It is frequently encountered in survival analyses based on birds shot, but it does not imply that the mortality rates for adults calculated from such data are wrong.

Population dynamics

The somewhat precarious status of the redhead on the North American continent should encourage us to obtain a picture of its population turnover as soon as possible. Two important statistics need to be carefully ascertained before this can be done with reliability: (1) an accurate field appraisal of the average ratio of juveniles to adults in the population at the start of the hunting

Table 33.—Abridged Life Tables of Redheads

Based on hunters' reports of birds banded as young before September 1. The data on the left are based mostly on birds banded in Utah; the more recent data on the right include banding work in Canada. Mortality rates are per cent per annum.

Age Interval (in years)	Part A			Part B		
	Dynamic Life Table			Time-specific Life Table		
	Number Reported Shot	Alive at Mortality Start of Year	Rate (q_x)	Number Reported Shot	Calculated Mortality Mortality Rate	(q_x)
0-1	410	471	87	537	487	91
1-2	40	61		50	23	
2-3	14	21		27	15	49
3-4	3	7		12	-	
4-5	1	4				
5-6	0	3				
6-7	0	3	54			
7-8	0	3				
8-9	1	3				
9-10	0	2				
10-11	0	2				
11-12	0	2				
12-13	2	2				
Adult Totals and Means	61	113	54	77 ^{1/}	38	49
1/ excluding age 3-4						

season, and (2) a better approximation of the mean adult mortality rate than the one obtained in this study. The need for these data can be illustrated by setting forth the population dynamics of this species with the statistics and estimates currently available.

Age ratio on September 1.—J. B. Low (1940) has used the ideal field technique to obtain an estimate of the age ratio in a redhead population at the start of migration. This involves a careful census of the breeding pairs on a series of study areas and close follow-up observations to determine the number of young that hatch, reach the flying stage, and subsequently leave the area. Low (1940) concluded that on his study areas in Iowa in 1938 approximately 380 young succeeded in entering the fall migration and that this number represented an average of 3.8 juveniles per breeding pair. The sex ratio obtained by Low (1941) for a 3-year period was 1.42 males to 1 female among 3400 redheads. This would imply that for each 200 adults only 166 could be mated. If 83 such pairs each averaged 3.8 juveniles, the 315 young thus produced (83 x 3.8) would

represent a ratio of about 1.6 young ($315 \div 200$) per adult. This ratio is subject to two possible refinements. A correction for failure of some females to mate might be made. I regard this as probably unnecessary. A second correction would be made to allow for mortality in the adults that were censused at the start of the season. Bearing in mind an annual adult mortality rate of the order of 55 per cent for this species, 4 per cent per month is not too absurd an estimate. For a 3-month period, this could be roughly construed to mean a 12 per cent decrease from 200 adults censused on June 1--a drop of 24 birds, leaving 176 alive on September 1. The ratio of 315 young to these 176 is 1.8 to 1. This may be regarded as an upper limit that could be considered in population analyses of this species.

Vulnerability of the young.--In discussing the relative vulnerabilities of adults and young to the gun, we can in the case of the redhead usefully assume that some of the results may well be due to differences in migratory behavior. Vulnerability in this species changes chronologically as well as geographically. For 372 Utah redheads (table 31) shot in September and October, 6 juveniles were bagged for every adult; for 122 shot from November to January inclusive, this ratio was 2.5 to 1. Taken geographically, these ratios are 33 to 1 for 171 birds shot in Utah, 3.4 to 1 for 166 birds shot in southern Canada and northern United States, and 2.6 to 1 for 83 shot in Mexico and the southern states. For Canadian-banded redheads (table 32), 3.2 young per adult were reported among 42 shot in Canada, 1.1 per adult among 64 shot in the northern tier of states, and 0.9 per adult among 72 shot farther south.

If the age ratio in the population is about 1.8 juveniles per adult on September 1 (as a purely preliminary estimate) and the age ratio is 4.2 to 1 in hunters' bags (table 33, part A), it follows that juveniles are more than two times as vulnerable to gunning as adults are throughout the entire hunting season (that is, $4.2 \div 1.8 = 2.3$).

Annual mortality rates.--A rough approximation of the age ratio on February 1 can, I think, be implied from the adult mortality rate in this species. With about 55 per cent of the adults dying each year, stable populations will need to consist of 55 young for each 45 adults at the start of the breeding season (or at the end of the hunting season when adult and juvenile mortality rates become equal). We can then readily calculate a true annual mortality rate for young birds from these statistics--

alive at start:	180 young	- 100 adults	(1.8 y/ad.)
alive end of year:	55 young	- 45 adults	(1.2 y/ad.)
number dying	125 young	- 55 adults	(2.3 y/ad.)

Under these conditions, the young undergo an annual mortality rate of about 69 per cent ($125 \div 180$). One important condition assumed here is that the population is remaining stable throughout the period of study. Because the best available sample for study here included birds only banded from 1926 to 1933, the shortness of this period should alert us to the possibility that the actual population from which these banding records originate may not necessarily be a stable one.

Another questionable point involves an age ratio of 1.8 young per adult on September 1. A ratio of 1.6 is also possible. This would result in an estimated mortality rate of 66 per cent for the young birds, instead of the 69 per cent above.

Similarly, if the adult mortality rate is about 50 per cent per year in this species (table 33, part B), juvenile mortality rates can be expected to lie between 69 and 72 per cent according to the two age ratios we have been considering for birds alive on September 1. The evidence we have available thus points to a mortality rates of about 70 per cent for young birds from September 1 to August 31, and to adult mortality rates of the order of 50-55 per cent per annum.

Percentage taken by hunting.—The possibility of a stable population here at least permits us to explore certain other parameters. Granting that juveniles are 2.3 times more vulnerable than adults are to the gun and that 4.2 times as many young are shot than adults, it can readily be shown that a 20 per cent adult hunting mortality rate will yield a series of statistics that satisfy the various age ratios we have determined. This in turn implies a 45 per cent hunting mortality among birds of the year:

	<u>No. Young</u>	<u>No. Adult</u>	<u>Ratio Yg/Ad.</u>
Alive at Start (Sept. 1)	180	100	1.8-1
Per Cent Shot Hunting	45%	20%	2.3-1
Number Shot	82	20	4.1-1
Number Alive (Feb. 1)	98	80	1.2-1
Per Cent Dying Nonhunting	44%	44%	
Number Dying Nonhunting	43	35	1.2-1
Number Alive Aug. 31	55	45	1.2-1
Total Dying Year	125	55	
Mortality Rate	69%	55%	

These computations were carried out as though all hunting mortality occurs at each age level before any nonhunting mortality. This of course does not happen in nature. During the years when these banding data were accumulated, about 78 per cent of the hunting mortality suffered by juveniles took place between September 15 and October 31. Only 7 per cent of the juvenile kill was recorded in December and January. For the adult redheads, these statistics

were 61 and 15 per cent respectively. Since nonhunting mortality does in nature coincide at least in part with hunting mortality, the per cent dying from nonhunting in the above table will tend to be too high.

It seems to me remarkable that a 20 per cent adult hunting mortality should result from these calculations. While I suspect that this result is too low, there seems to be no way of verifying this at the present time. Higher hunting rates would make for declining populations--a possibility that seems quite real but is likewise unprovable at this writing.

Redhead populations other than Utah's.--The weak point in these analyses, as I see it, lies in the local origin of the data: a productivity estimate from Iowa, banding statistics from Fish and Wildlife Service operations in Utah, bag information from Hochbaum's work at Delta, Manitoba. Perhaps certain segments of the redhead population have been subjected to mortality rates of the order postulated here. It surely does not follow at this time that the data hold for all segments of this species' population. As a critical test for this, I assembled 223 mortality reports of redheads banded outside of Utah up through the year 1941 (table 34.). Even when birds banded in the hunting season are included in the sample, a very high proportion of the reports cover birds shot in their first year of life. Although this proportion may be lowered slightly by subsequent reports of birds shot as adults, we must conclude that the extraordinary population turnover of redheads pictured for Utah birds is not a local phenomenon.

The importance of a correct adult mortality rate in these calculations should not be overlooked. All samples cited here in this connection were small. The mean mortality rate of Utah-banded redheads (54 per cent, table 33, part A) was based on 61 birds; that for the non-Utah birds (47 per cent, table 34) was based on 47. Seventy-three others banded as adults gave a mean annual mortality rate of 62 per cent. It is entirely possible that these rates reflect not only sampling errors but also changes in hunting regulations. A 55 per cent overall adult mortality rate seems like a reasonable yardstick under the circumstances.

All this evidence leads me to conclude that redheads in North America have in the past sustained a juvenile hunting kill of the order of 50 per cent, that the adult kill has been 20 or 30 per cent and that annual mortality rates have been about 70 per cent for juveniles and about 55 per cent per year for adults. Under these conditions, the population would remain stable only if each pair produced about 3.6 young as of September 1.

Table 34.—Hunters' Reports of Redheads Banded Outside of Utah

Unless otherwise noted, these birds were banded as late as September 10. All were marked as juveniles. The last year of banding was 1941; only 5 years of complete data were available at the time the table was compiled, the x in some cells of the table indicating the age interval where the data are incomplete.

Where Banded	Number Reported Shot by Age Intervals (in years)							Total Adults
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	
Manitoba	35	2	4	0	2	x	x	43
Manitoba 1/	45	1	1	3	1	x	x	51
Oregon	10	5	3	2	0	0	0	20
California	4	1	2	1	0	0	x	8
Montana	0	0	0	3	0	0	0	3
North Dakota 2/	49	5	4	0	0	x	x	58
South Dakota	29	1	3	2	0	0	1	36
Iowa	4	0	0	0	0	0	x	4
Total No. Shot	176	15	17	11	3	0	1	223
Alive at Start	223	47	32	15	4	1	1	323
Mortality rate	79							47

1/ banded throughout September (by R. D. Harris of Ducks Unlimited, Canada)

2/ banded to October 29 (mostly by S. H. Low and C. J. Henry, Fish and Wildlife Service)

Summary

Of 406 redheads banded as young in Utah and shot in their first year of life, 78 per cent were shot in the first 6 weeks of the hunting season, 41 per cent of them being reported in Utah; when Utah was excluded, 49 per cent were shot in this same period. This early-season kill was less pronounced in Canadian-banded samples, but still rather high.

An abridged life table for 471 juveniles banded mostly in Utah and later reported shot yielded the same high proportion of reports in the first year of life (87 per cent) as previously reported by Williams (1944). This high ratio of juveniles to adults was found to be very close to age ratios obtained from hunters' bags in Manitoba by Hochbaum (1944). A parallel but less striking condition was reflected in banding statistics for 223 redheads from other parts of the continent.

Using a crude approximation of the age ratio (1.8 juveniles to 1 adult) in the living redhead population at the start of the hunting season, the overall annual mortality rate for young birds was estimated to be of the order of 70 per cent for their first year starting September 1. The mean annual mortality rate for adults is believed from small samples to be around 55 per cent.

It can be shown from these Utah statistics that, if only 20 per cent of the adult redheads was taken by hunters, then the population probably remained stable during the banding period 1926-33. If more than 20 per cent was taken, then the population declined. A 20 per cent adult kill by hunters is taken to imply a 45 per cent hunting mortality among birds of the year. While the vulnerability of this age class seems to be somewhat further exaggerated by different migratory behavior among both adults and young, it nevertheless is very real and an important problem in the conservation of this species. Records of redheads more recently banded in Canada yield a picture of mortality generally similar to that found for birds banded in Utah.

Chapter VII.--Order Falconiformes: Vultures, Hawks, and
Their Allies (Family Accipitridae: Hawks
and Eagles)

Marsh Hawk

Literature on productivity and survival

Merrill C. Hammond and C. J. Henry (1949) have compiled some very pertinent nesting statistics on Circus cyaneus. In North Dakota, 60 clutches were observed to average 5.1 eggs in number; 43 nests with young were found to hatch an average of 4.1 young; and 3.2 birds fledged from 11 nests. The age at which the birds breed is not known with certainty.

Banding work in North America

Young marsh hawks have been banded by 108 persons whose work was represented by recoveries in the files of the Fish and Wildlife Service at the time of this study. I did not ascertain the number of persons who banded birds of this species but failed to get recoveries. The recovery reports that I examined originated from 6 Canadian provinces and 21 states in the United States. The more important banders were W. R. Salt of Alberta, C. J. Henry and M. C. Hammond of North Dakota, C. E. Holcome of Illinois, and L. W. Campbell of Ohio. Passage birds, adults, and young tethered for experiments were excluded in this inventory.

Characteristics of the sample studied

The dispersal and migratory tendencies of this species may be seen in the following tabulation of birds reported shot (* means that the band was sent in to the Fish and Wildlife Service; # means that I could not locate the letter supporting the record):

<u>Where Banded</u>	<u>Where Reported Shot</u>
Alberta	Id., Wash., Wyo.
Saskatchewan	La., Mo., Okla. (3), Tex. (4), Wash.
Manitoba	N.D.
Utah	Ariz.
Colorado	Tex.
Wyoming	Calif.
North Dakota	B.C., Kan., La. (2), Mexico, Mo., Tex. (?)
South Dakota	Cclo., La., Mo. (2), Okla. (2)
Minnesota	Cuba, Ia., La., Mo., Okla., Tex. (3)
Wisconsin	Ark., Ill. (4), Ind., Kan. (2), Ky., La. (3), Miss., Mo., Neb. #, Tenn., Tex. (2)

<u>Where Banded</u>	<u>Where Reported Shot</u>
Illinois	Cuba, Ga., Ind., La., Mich., Tex., Wis.
Ontario	Ala., Ark., Fla., Ga., Ill., Ky., Mich., Mo., N.C. (2), Okla. Tenn.
Michigan	Ill. (3), Ind. (3), Ia., Kan.*, La., N.C., Okla., Ohio (2)
Indiana	Ala., Ill., La., Mich.
Ohio	Ark., Ill. (2), Ind. (2), Ky. (2), Mich., Miss., Mo., Okla (3), Ont., Pa. (2), Tex. (4)
Quebec	N.Y., Prince Edward Is., Vt.
Massachusetts	N.Y.

Banding operations up through 1941 yielded 161 reports of birds being shot (5 of them in July were later excluded from life-table analyses), 7 reports of birds found dead, 6 found wounded, 7 caught in mammal traps, 10 captured, and 15 reports of a vague or indefinite nature. Of 102 birds shot in their first year of life (August 1 to July 31) and reported with definite recovery dates, 80 per cent were apparently shot in the first 5 months. For 48 adults reported shot, this value was 56 per cent (table 35). It would seem probable that a life table based on this type of sampling would exaggerate the mortality rate for the first year of life.

Table 35.--Months in Which Marsh Hawks Were Reported Shot

Age When Shot	Number Classified by Month Reported												Total Shot
	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	
First Year	18	21	16	19	12	6	4	2	1	1	2	0	102
Adult	3	3	9	10	2	3	4	3	3	3	2	3	48

Abridged life table

A preliminary life table based only on birds shot is set up in table 36. The addition of 30 birds found dead or wounded or captured in various ways would not significantly change the mortality rates of 59 per cent for birds of the year and 30 per cent for adults. (A preliminary life table based only on these 30 would give a first-year mortality rate of no more than 67 per cent.)

Age ratios and productivity

Column l_x in table 36 implies that 135 adults are needed to raise 99 birds each year. This is an age ratio of the order of 0.7 young (0.73) per adult or 1.5 young per pair alive on August 1.

While the occurrence of a single bird aged 16-17 in table 36 is a perfectly valid indication of the age which this species can and does obtain in nature, this single individual would

Table 36.—Age Intervals in Which Marsh Hawks were Reported Shot

Based on birds banded as nestlings prior to 1937; a small and probably insignificant number remain to be reported past age 9-10; each year starts August 1. The letter x below means that full data for this age interval were not yet available when the table was compiled.

Age Interval (in years)	(d_x) Number Shot	(l_x) Number Alive Start of Year	(q_x) Mortality Rate per Year
0-1	58	99	
1-2	13	41	
2-3	10	28	
3-4	5	18	
4-5	3	13	
5-6	3	10	
6-7	2	7	
7-8	2	5	
8-9	0	3	
9-10	2	3	30%
10-11	x	(1)	
11-12	x	(1)	
12-13	x	(1)	
13-14	x	(1)	
14-15	x	(1)	
15-16	x	(1)	
16-17	(1)	(1)	
Total	99 (+ ?)	234	42%

appear to be atypical of samples of 100 marsh hawks. Its elimination from consideration in the above age ratio would raise the number of juveniles in the population to 0.8 per adult on August 1. Although this is still subject to sampling aberrations, it can be used to obtain a working explanation of marsh hawk vital statistics as they are now discernible.

The productivity of marsh hawks in North Dakota ran about 3.2 young able to fly per successful nest (Hammond and Henry 1949). Roughly 70 per cent of their nests fledged one or more young, 16 successful and unsuccessful nests fledging an average of 2.2 young per nest. Such a scale of productivity represents a mean of 1.1 young for every breeding adult that started the nesting season.

Population dynamics

How can an age ratio of the order of 0.8 (or 0.7) juveniles per adult on August 1 be explained in the face of a productivity of 3.2 young in the fledging stage in successful nests? If the mortality rates in the life-table analyses here are even approximately correct,

two factors potentially controlling the population need to be considered: (1) extremely heavy mortality suffered by the young birds when they leave the nest, and (2) delayed sexual maturity. The following calculations will demonstrate the limitations of these postulations and the kind of field data still needed to make our picture of the population dynamics of this species a definite one.

Population equilibrium when all birds breed at one year of age.--If for each pair of breeding adults alive at the start of the nesting season, 2.19 young are fledged (Hammond and Henry 1949) the true age ratio in the population at fledging time will be modified by adult mortality during the nesting period. I take this period to be about 2 months. Since adult mortality is about 30 per cent per year, in 2 months roughly 10 per cent of the adults die. It follows then that the age ratio at fledging time is 2.19 young per 0.9 pair; that is, 2.43 young per pair or 1.2 young per adult. With a median fledging date of about July 10 (my estimate), the young would have to suffer a minimum 33 per cent mortality in the next 3 weeks in order to reach the life-table age ratio of 0.8 per adult. This postulated mortality seems to me to be too high. I therefore regard the hypothesis of breeding at one year as not sustained at this time.

Population equilibrium when all birds begin to breed at 2 years of age.--Under this hypothesis, the 41 birds alive at the start of age interval 1-2 in table 36 are nonbreeding. The 99 young alive at the start must then be produced by 94 adults; this means a life-table age ratio of 1.05 young per adult on August 1. This may now be compared to the age ratio of 1.2 per adult (as of about July 10) inferred from Hammond and Henry's work. To drop the 1.2 value to 1.05 would require a minimum juvenile mortality of 12.5 per cent over and above that sustained by the adults. I do not believe that this 12.5 per cent is a reliable estimate of what takes place in nature. All the samples (productivity and life table) are small enough to involve fairly large sampling errors. We can, however, conclude that initial breeding at 2 years of age offers the best available explanation of vital statistics for this species as we now know them.

Some confirmation of this situation is found in the plumage descriptions of marsh hawks. According to Bent (1937, p. 84), the juvenal plumage is worn for about one year, and the adult plumage is usually acquired by a complete molt that takes from July to October or later. In my experience with the duck hawk or peregrine falcon (which has an identical type of molt), such immature birds are readily accepted as mates but the females either lay no eggs or have very small clutches. It seems to me entirely possible that this situation is likewise true of the marsh hawk. With so few banding recoveries available for the precise calculation of subadult and adult mortality rates, and with the probability that some band loss may mar the results, we are not able to say with certainty that all one-year old marsh hawks raise no young. Quantitative studies of nesting success and productivity from various parts of this species'

range are still needed to complement the nesting statistics reported by Hammond and Henry (1949) and make this general picture of population dynamics a reliable one.

Summary

Of 102 marsh hawks shot in their first year of life (August 1 to July 31), about 80 per cent were shot in the first 5 months. For 48 adults reported shot, this value was 56 per cent. During this first year of life, a mortality rate of the order of 60 per cent was indicated in a sample of 99 birds. The mean adult mortality rate in this small sample was 30 per cent. While both these statistics must be considered as preliminary results only, they appear to imply that marsh hawks one year old contribute very little to the annual production of young.

Chapter VIII.--Order Charadriiformes (Family Laridae:
Gulls and Terns)

Caspian Tern

Literature on productivity and survival

A. H. Miller (1943) in a census of a colony of Hydroprogne caspia found the mean number of eggs in 325 nests to be 1.8. In the same colony 51 other eggs were scattered about outside of the nests. Miller found the average number of young to be 1.5 in 37 nests.

The age at which this species breeds seems to be unknown. O. L. Austin, Jr. (1932) and O. L. Austin (1942) in their work on a smaller bird, the common tern (Sterna hirundo), found that an appreciable fraction of the younger birds do not appear to begin breeding until they are 4 years old.

According to Ludwig (1942), the greatest mortality among banded caspian terns occurs in the first 6 months of life.

Banding work in North America

Of the more active banders working from 1926 to 1941 on this species, F. C. and C. C. Ludwig ringed 4650 birds for 53 recoveries, W. I. Lyon ringed 4257 for 71 recoveries, Adam Brown ringed 1426 for 10 recoveries, and H. E. Alcorn ringed 1063 birds for 6 recoveries. Recovery rates for 9 successful banders were 2.1 per cent for 3305 birds banded 1926-32 and 0.9 per cent for 8786 ringed from 1933 through 1941. Only recoveries reported up to August 31, 1946, were included in these totals.

Characteristics of the samples studied

The monthly variation in recovery reports (table 37) discloses no important differences between first-year and older birds. They may, of course, appear when a larger sample is available.

Most of the caspian tern recoveries originated from Great Lakes bandings. There is an obvious migration of these birds to Lake Erie, thence overland to the Atlantic coast (Long Island to Chesapeake Bay), and so south to Florida and the West Indies. Important wintering grounds for both young and adults include Florida, Louisiana to Alabama, and Colombia. The lack of reports from Mexico suggests that Colombia is not reached by following the coast. An excellent picture of this migration has been given by Ludwig (1942).

Abridged life table

Table 38 represents a preliminary estimate of mortality based on only 106 caspian tern recoveries. Of these, 71 were

Table 37.—Monthly Variation in Recoveries Reported for Caspian Terns Birds Banded from 1922 to 1941
(Frequency by months, August to July)

How Obtained	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	Total
In first Year													
Shot	-	3	2	5	1	2	-	-	1	1	1	-	16
Found dead	5	9	10	6	1	5	3	2	0	3	4	1	49
Captured	4	8	-	2	3	3	-	-	1	-	1	1	23
Total	9	20	12	13	5	10	3	2	2	4	6	2	88
As Older Birds													
Shot	2	-	-	8	3	4	1	-	-	1	-	4	23
Found dead	7	9	11	1	3	4	4	2	3	4	1	3	52
Captured	2	5	2	1	2	2	-	2	1	2	2	-	21
Total	11	14	13	10	8	10	5	4	4	7	3	7	96

reported found dead, 30 were reported shot, and 5 taken by scientific collectors for 5 different museums in the United States and Canada. Some of the dead birds in table 37 were excluded here because they were banded in 1922 to 1925 when the durability of bands was subject to doubt.

This small sample yields mortality rates of 44 per cent per year for the first year of life, 26 per cent for the second year, and a mean of 18 per cent per year for age intervals past this point. Mortality rates calculated for age intervals from 2-3 to 8-9 show no wide fluctuations, the actual rates varying from 11 to 17 per cent per year and the mean for these 7 age intervals being 15 per cent (14.5).

This table involves small numbers, some of which exhibit sampling errors that are further distorted by the statistical method employed here to set up a mortality series. An examination of the survival curve (figure 9) on semilogarithmic paper further emphasizes the inadequacy of the data. The survival curve begins to drop after age interval 8-9, suggesting band loss. Had the curve continued with the same slope, the population would not have been reduced to one per cent until age 27-28. Failure of the birds in table 38 to attain such an age may be also due in part to the extremely low recovery rate, as well as the absence of very large banding operations in the early 1920's.

Age ratios and productivity

The age ratio of the population shown in column 1^x of table 38 cannot be critically evaluated without some knowledge of the age at which most caspian terns begin to breed. If all the adults in this table breed at age 3-4, each pair would have to raise 1.1 young to August 1 to keep the population stable. This can be compared to 1.5 young per successful nest noticed by Miller in 37 nests on the

Table 38.—A Preliminary Life Table for Caspian Terns

Based on nestlings banded from 1926 to 1941 inclusive, each age interval starts August 1. The mortality series (column d'_{x}) represents the number reported dead per 10,000 birds available for study at each age interval; from this, a survival series (column l'_{x}) has been constructed to represent the number known to be alive at the start of each age interval.

(1) Age Interval (in years)	(2) Banded Birds Available	(d_x) Number Reported Dead	(d'_{x}) Mortality Series 10,000 [$d_x \div (2)$]	(l'_{x}) Survival Series	(q_x) Mortality Rate (per cent per year)
0-1	12,091	52	43.0	97.0	44
1-2	12,091	17	14.1	54.0	26
2-3	12,091	7	5.8	39.9	
3-4	12,091	6	5.0	34.1	
4-5	12,091	5	4.1	29.1	
5-6	11,032	3	2.7	25.0	
6-7	10,534	4	3.8	22.3	18
7-8	9,631	3	3.1	18.5	
8-9	8,850	2	2.3	15.4	
9-10	7,465	3	4.0	13.1	
10-11	5,884	1	1.7	9.1	
11-12	4,811	1	2.1	7.4	
12-13	3,758	2	5.3	5.3	
13-14	3,305	0	0	0	-
Total	-	106	97.0	370.2	

Pacific coast; it implies that nearly 80 per cent of all the adults above age 2-3 would have to be successful in raising young. Both samples are so small that the comparison has a limited value only.

Theoretical populations having a straight 15 per cent mortality rate for all age intervals past 2-3 apparently are balanced by productivity only slightly lower than this one. This would permit a larger fraction of the adults to be either nonbreeding or unsuccessful in bringing off young.

Published survival studies of other Laridae

Herring Gull

Abridged life tables have been published for *Larus argentatus* by Marshall (1947) and by Paynter (1947, 1949). Some of their results are compared in table 39 along with statistics on the European herring gull reported by Paludan (1951). This

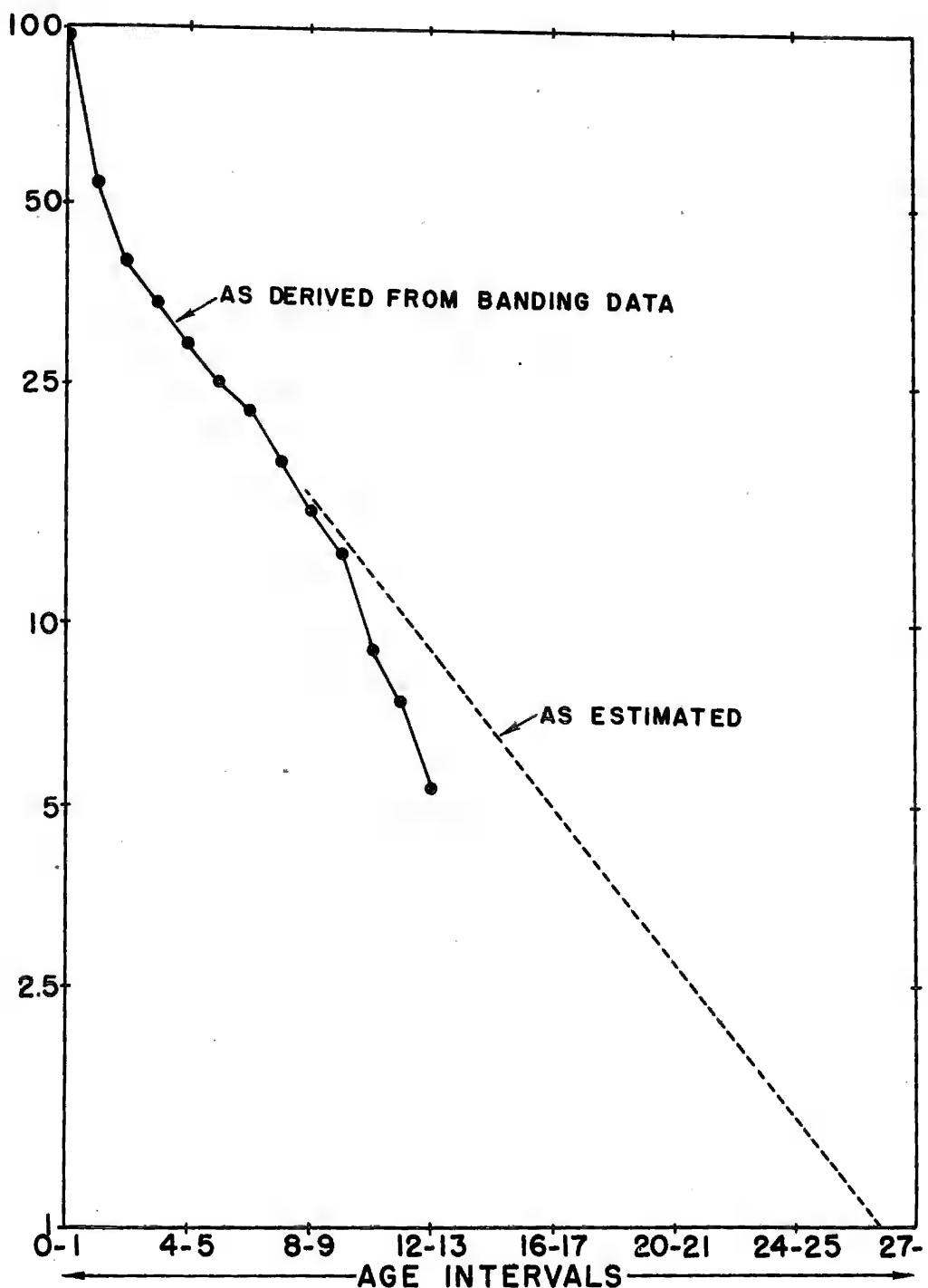


Figure 9.--A Caspian Tern Survival Curve

Table 39.--Published Mortality Rates for Herring Gulls

Each rate is here expressed as per cent per year. Marshall (1947) and Paludan (1951) used a life table starting as of September 1. Paynter (1947) claimed that his first table started as of July 1. Subsequently he reported that it and a second series of mortality rates hold for years starting "sometime" in early August (Paynter 1949, p. 161).

Age Interval	(a) Marshall (1947)	(b) Paynter (1947)	(c) Paynter (1949)	(d) Paludan (1951)
0-1	60	42	50	62
1-2	38	31	41	22
2-3	29	24	28	19
3-4	29	21	23	16
4-5	39	29	35	14
5-6	48	35	27	17
6-7	39	41	17	13
7-8	28	32	19	17
8-9	1/	58	28	16
9-10	1/	100	14	16
10-11	1/	-	100	9
"adults" 2/	35	30	32	17

1/ not calculated (small sample); last bird died at age 16-17

2/ excluding age 0-1; my calculations

last paper appeared too late for consideration in this report. It is a model study, and I believe the low mortality rates cited point up the inferior bands used here in America.

Are these discrepancies in the American results principally due to differences in computation and analysis; or do they represent real differences between (a) a generalized sample of 3806 herring gulls banded at various places in North America from 1921 to 1939 inclusive (= Marshall's sample), (b) a specific sample of 1252 banded in New Brunswick from 1934 through 1943¹ (= Paynter's first sample), and (c) 362 birds banded in New Brunswick in 1936 and recovered up to June 30, 1946 (Paynter's second sample)?

(a) Starting dates.—Marshall (1947) started each age interval as of September 1. Paynter (1947) claimed that his first table started as of July 1, the date when banding of nestlings

¹1943 is not specifically mentioned by Paynter as the last year of banding work he used. The use of any subsequent work would create an important bias in his analysis.

became practical. This would seem to include mortality in the nest, but Paynter (1949) subsequently pointed out that bands found on dead nestlings were removed and placed on live birds "so that, as nearly as possible, every banding record represents a fledged bird." His life tables based on banding data thus begin "sometime in early August" (Paynter 1949). The actual difference in starting dates thus appears to be a small one.

(b) Banding dates.—Marshall (1947, p. 192) used birds banded through 1939. Since his paper was published in April 1947, his returns must have been those available as of September 1, 1946 at the very latest. Birds banded as late as 1939 could, therefore, contribute to no more than the first 7 age groups in his life table. The mortality for at least the last 10 age groups (7-8 to 16-17 inclusive) is thus not completely represented. This error tends to raise the apparent mortality rates for the early years somewhat slightly and for the later years somewhat importantly. Paynter sought to avoid this error by dividing his recovery series by the number of years for which reports were available.

The validity of Paynter's adjustment in 1947 depends on the assumption that practically the same number of birds are banded each year. Quite to the contrary, the work of the Bowdoin Scientific Station did vary widely from one year to another. The extensive banding operations early in the Bowdoin program thus left an unduly large number of older birds in Paynter's recovery series. This is clearly the reason why his mortality rates as published in 1949 tend to be higher than those he published in 1947.

The banding dates in Paynter's 1949 paper are confined to the year 1936 and the recoveries include only those received "up to June 30, 1946." Paynter calls this an 11-year study. In a sense this is so, but only 10 full yearly age intervals are thus possible for life-table compilation, and one wonders how he obtained 11 (table 7, Paynter 1949, p. 162). This of course introduces only minor errors in the calculations. It is curious that Farner (1945), Marshall (1947), and Paynter (1949) have all committed this oversight, but that none of the Europeans have.

(c) Type of life table.—When I arrived at the Patuxent Research Refuge, rubber bands still enclosed the mortality reports that Marshall quite evidently had used. Except in one instance, I found that he and I did not differ importantly in interpreting what constituted a valid record of a bird reported to be found dead. For birds banded from 1923 to 1933, however, 2.5 per cent of the cards had not been completed and placed on file; most of these were from age 9-11 to 15-16, and all could be pardonably overlooked by a visiting investigator. Adult mortality rates calculated by Marshall thus tended to be too high. Marshall used only reports of birds found dead, and upon these he constructed a dynamic life table following Lack's method exclusively.

Paynter's first life table for herring gulls is based upon the results of an extremely interesting analysis of his

1252 records, which he broke down into 674 "natural recoveries" (birds found dead presumably from natural causes) and 578 "artificial recoveries" (mortality due to man, birds captured alive, vague records). Three statistical objections to his interpretations of this breakdown have already been mentioned under "Internal Comparisons" in Chapter III. It is merely necessary to add here that 803 reports of birds dead, 311 reports of birds captured, caught, found ill, or observed, and 138 others of a vague category (band recovered--11, no information--23, "found"--58, etc.) were subsequently used as a mortality series. Although Paynter may well be justified in assuming that some of these 311 birds died the year they were captured, this may not be true of all of them (such as 54 caught by fishermen and 25 "captured and released"). Captured birds make up 25 per cent of his sample. It is interesting to note that under similar circumstances Dutch investigators would regard all 1252 records as birds known to be alive at the start of the year in which they were recovered, and that they therefore would analyze them as a survival series in a time-specific table. Paynter's decision to use these records as mortality data in a dynamic life table, instead of a time-specific one, at least produces minor statistical distortions that should be clarified and justified.

In the hope of shedding some further light on Marshall's results, I constructed a life table based on birds banded from 1925 to 1930 inclusive (table 40). These reports were not checked against banders' schedules.

The 60 per cent first-year mortality rate here is identical to the 60 per cent found by Marshall, but the mean mortality rate for later years (27 per cent) is lower than his data (35 per cent) indicate. The difference in survival curves is clearly evident in figure 10 where--after age 10-11 in the 1925-30 curve--the apparent mortality rate seems to be increasing. If this was a band-loss effect and the adult mortality rate was constant at all ages, a straight line running from age 1-2 or 2-3 could be extended through the point at age 10-11 and intercept the 1 per cent line close to age 23-24. Under these circumstances, the inference is that, among every 500 birds (504 in table 40) alive on the September 1 following their hatching, one individual in every 500 presumably would live to this advanced age. This correction for band loss suggests an adult mortality rate of 25 per cent per year. In Europe where the banding program is much older, herring gulls have been known to reach at least 25 years of age in the wild (Schütz 1935; Paludan 1951).

If all herring gulls breed at age 3-4, the 414 adults in table 40 would need to raise 2.4 young per pair to September 1 to keep the population stable. With a band-loss correction as indicated above, this productivity would have to be about 2 young per pair. Preliminary nesting data secured by Paynter (1949) indicated a mean productivity of less than one fledgling per nesting pair in the heavily crowded Kent Island (N.B.) colony in 1947. The life-table results obtained here cannot, therefore, be accepted at this time.

Table 40.—An Abridged Life Table for Herring Gulls

The birds were banded as young in nesting colonies during the years 1925 to 1930 inclusive, but the data were not checked against the banders' original reports. Each age interval starts September 1. Reports past age 15-16 were not available at the time this table was compiled.

(x) Age Interval	(d _x) Found Dead	(l _x) Alive at Start of Year	(q _x) Mortality Rate Per Cent Per Year
0-1	302	504	60
1-2	59	202	29
2-3	30	143	21
3-4	31	113	27
4-5	21	82	
5-6	23	61	
6-7	8	38	
7-8	4	30	
8-9	6	26	
9-10	5	20	27
10-11	3	15	
11-12	5	12	
12-13	2	7	
13-14	1	5	
14-15	3	4	
15-16	1	1	
Total (all ages)	504	1263	40
Total (3-4 to 15-16)	113	414	27

Paynter (1949) has calculated that a mean (adult?) mortality rate of 14.5 per cent per year would be sufficient to balance the low productivity he encountered at Kent Island in 1947. This rate differs only slightly from the uncorrected adult mortality rate obtained for caspian terns in this chapter and from an overall annual rate of 17 per cent obtained by Paludan for European herring gulls past their first year of life; it therefore seems to me to be within the realm of possibility. The next life-table study of North American herring gulls will, I hope, contrast the results from fresh-water banding operations against those carried out under marine conditions. This approach may throw some additional information on the band-loss complications that appear to have been encountered here.

Among the conflicting statistics now available for this species are the annual mortality rates for young birds (as of their first September 1 or fledging date "in early August"). These run 42 per cent (Paynter 1947), 50 per cent (Paynter 1949), and 60

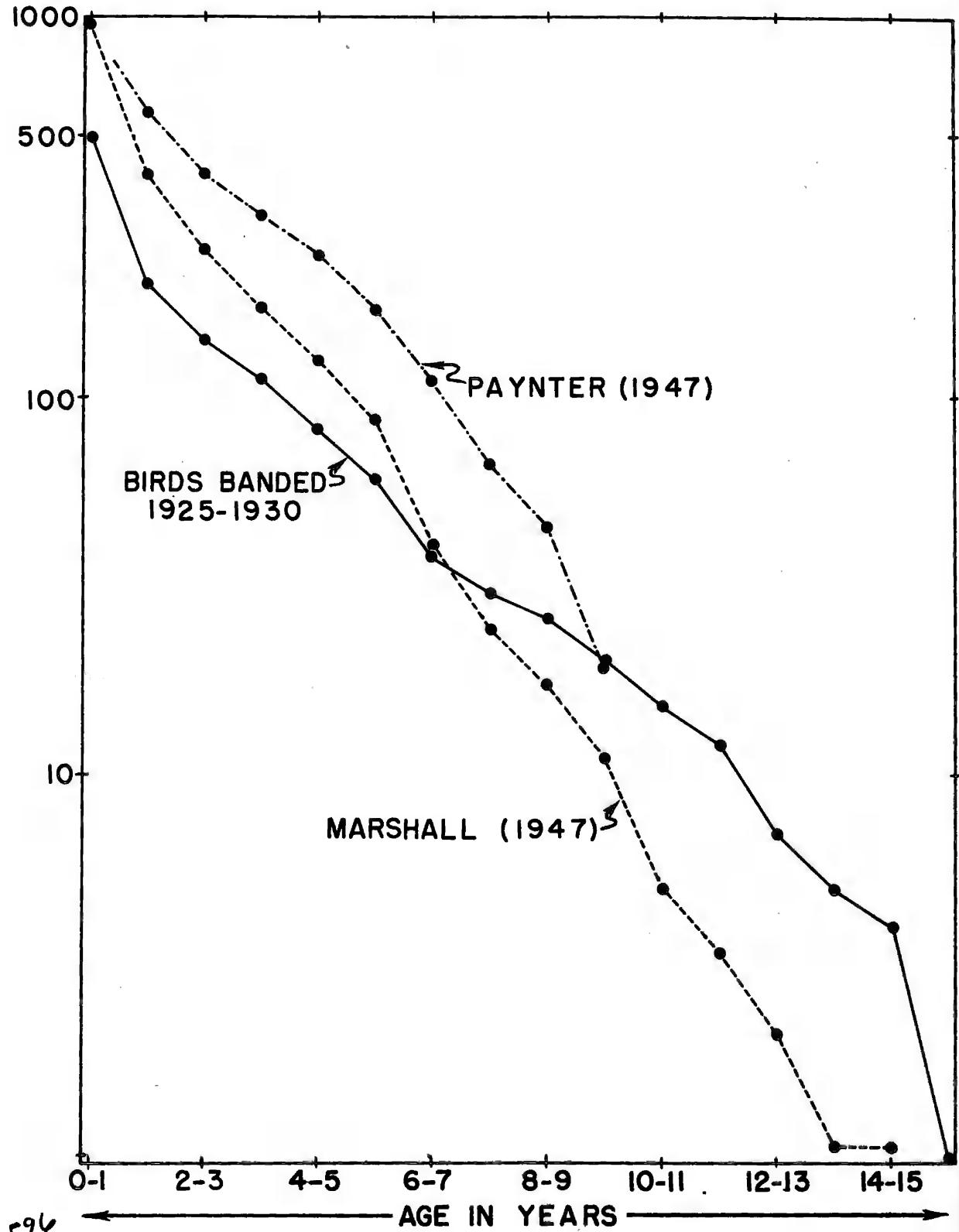


Figure 10.—Abridged Survival Curves for Herring Gulls

per cent (Marshall 1947; Paludan 1951; and this paper). The mere agreement of these last three on this point does not prove our respective life tables are reliable; each may be subject to the same kind(s) of bias. Both band loss and/or vulnerability to shooting could make the first-year mortality rate calculations too high. It is my feeling that, whatever the reason, this exaggeration is present in table 40.

Common Tern

The life span and age structure of *Sterna hirundo* populations on Cape Cod, Mass., have been analyzed in considerable detail by O. L. Austin (1938, 1942, 1945, 1947a, 1947b, 1949) in a series of reports that are still in progress. In the last of these, Austin mentions a "high" mortality rate of 17.2 per cent per year apparently obtained from a preliminary statistical analysis that is to be discussed in a future contribution.

Austin is now working up the results of what is the most extensive population study ever undertaken in ornithology. Up to the present, he has published only on his retrapping data. The life span and age structure of his populations are invariably presented on a time-specific basis, such as those found in the population for the year 1938, or the years 1938-41. The reliability of this picture depends not only on absence of band loss (which Austin has worked hard to overcome) but also on sampling errors (which he shows are small) and on corrections for variations in the numbers originally banded (a point that I feel he has overlooked). The nature of these variations is evident in column (2) of table 41.

Austin (1942, 1945, 1947a) has mentioned the life span of the common tern as being 10 years, with a small number persisting even later in the population. "Life span" like the "turnover period" is a term that always should be carefully defined. "On a graph made of the percentages of birds banded as chicks which return each year of their age," writes Austin (1945), "the points for all more than twelve years are below a base line indicating the presence of none." I find it hard to reconcile this statement with Austin's raw data that are reproduced as columns L_x and $L'x$ in table 41 and especially with column $L''x$ when it is transposed to semilogarithmic paper (figure 11). It appears to be contradicted further by other statements in this same paper (Austin 1945) that 1 out of every 200 adults is 13 or more years old and that the recording of ages past 18 years can be expected in subsequent retrapping operations.

It is perhaps worth re-emphasizing here that the recording of the disappearance of the last individual in any population is governed not only by biological laws but by statistical ones as well. The biological evidence now available points to no marked changes in annual mortality rate throughout most of a bird's adult life. Under such conditions, and with a given mortality rate, the

Table 41.—Disappearance of Common Terns in a Retrapping Program

The implied age structure of the Cape Cod nesting population found by Austin (1942) is given in columns L_x and $L'_{x'}$. Many birds do not nest until age 4 or 5 and so are unrecorded in the trapping program at the nesting colonies. Column $L''_{x'}$ attempts to weigh the returns in column L_x according to their availability as shown in column B. No correction was attempted to eliminate trapping inefficiency and thus permit calculation of mortality rates. These birds were banded as nestlings. $L''_{x'} = 10,000 (L_x \div B)$.

(x)	(L_x)	($L'_{x'}$)	(B)	($L''_{x'}$)	(?d _x)	(?a _x)	
Age When Retrapped (in years)	No. Nests trapped	No. Re- trapped of Total Nests	Per Cent ally Banded	No. Origin- ally Banded (1, 2, etc., yrs.before)	No. Dis- trapped Banded	No. Dis- appearing between Ages	Disappear- ance Rate (per cent per year)
1	44	1.7	30,580	14.4			
2	99	3.7	27,944	35.4			
3	417	15.7	29,620	140.8			
4	688	25.9	35,373	194.5	28.9		
5	566	21.3	34,170	165.6	68.9	42	
6	334	12.6	34,548	96.7	21.8	23	
7	226	8.5	30,180	74.9	34.6	46	
8	83	3.1	20,571	40.3	9.6	24	
9	62	2.4	20,212	30.7	5.4	18	
10	45	1.7	17,755	25.3	5.2	21	
11	30	1.1	14,906	20.1	5.3	26	
12	24	0.9	16,174	14.8	7.0		
13	12	0.5	15,461	7.8	-0.9		
14	11	0.4	12,330	8.9	1.3		
15	6	0.2	7,925	7.6	2.1		
16	2	0.08	3,962	5.0	5.0		
17	0	0	1,392	0			
18	0	0	392	0			
19	0	0	94	0			
Totals and means (age 5 to 16)				502.7	167.1	33	
Totals and means (age 6 to 9)				242.6	71.4	29	
Totals and means (age 10 to 16)				94.5	25.0	26	

disappearance of the last bird depends on the size of the statistical sample being studied. For 1000 common terns subject to the 32 per cent annual disappearance rate implied in figure 11 and under continuous annual observation from age 4 onward, the last individual should be recorded at age 25; for 500 adults, this would mean age 19 or 20; for 100 adults, this would mean age 18. If the actual mortality rate is 17 per cent as Austin (1949) says, the last individual would live very much longer. The recent report of a common tern at least 20 years old (Austin 1947b) surely is no surprise.

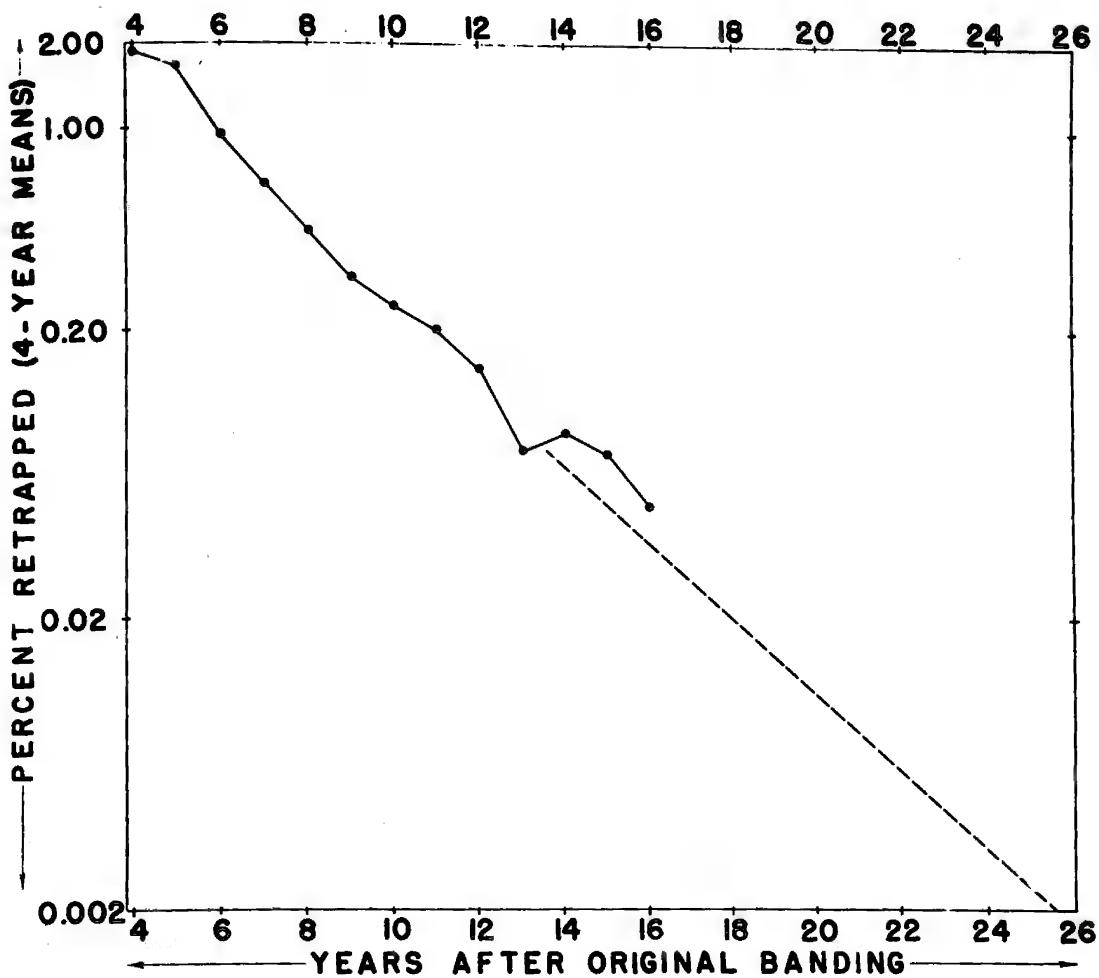


Figure 11.--A Survival Curve for Common Terns, Based on Percent Trapped (4-year means 1938-1941) after Austin (1942). Solid line represents retrap data, broken line potential survival.

In this examination of the published data on common terns, the trapping efficiency of Austin and his co-workers has not yet been mentioned. This is a very difficult statistic to calculate, and Austin (1949) has discussed its complexity in detail. Upon this point rests the precise calculation of a mortality rate from the retrap data; this is a task for the original bander, not a reviewer. In claiming that Austin's (1942) data suggest a fluctuating adult mortality rate varying from "178 to 636 per thousand even between the fourth and eighth years, when the numbers are large," Deevey (1947) was led sadly astray. These statistics await a future report by Austin on the records of banded common terns found dead by the general public. A comparison of such data with productivity statistics and returns obtained by retrapping should make a picture of population dynamics in this species finally possible. The great merit of Austin's work lies not only in the size of his samples and the continuity of his banding over a long period but also in his use of a retrapping program to replace bands on the older birds.

Summary

Caspian terns have been found to have a mean of about 1.8 eggs per nest and (in a sample of 37) 1.5 young per nest (Miller 1943). Survival studies of banded birds are handicapped by the extremely low recovery rate (about 2.1 per cent). A preliminary life table based on 106 birds yielded a mortality rate of 44 per cent for the first year of life and a mean of 18 per cent for all years past age 1-2; band loss after age 8-9 is suspected as a potential source biasing these statistics. The age at which this species breeds seems to be unreported, and the survival results on banded birds cannot be verified at this time.

Marshall's (1947) work on herring gulls was in part repeated. A 60 per cent first-year mortality rate was found to be identical to one he reported; a mean adult mortality rate of 27 per cent per year differed from a 35 per cent mean indicated by his data. Band loss after age 10-11 has apparently made both these statistics too high. Some critical objections are raised to Paynter's (1947, 1949) work on the same species.

In a brief review of Austin's (1942, 1945, 1947a) valuable work on the common tern, his time-specific tables are alleged to misrepresent somewhat the age composition of the populations he has been studying, the proportion of very old birds being apparently higher than he has indicated.

Chapter IX.—Order Columbiformes: Doves and Pigeons
(Family Columbidae: Doves and Pigeons)

Mourning Dove

Literature on productivity and survival

In terms of over-all nesting success, the productivity of Zenaidura macroura has been well studied (table 42). Although about 50 per cent of functional nests (those in which one egg has been laid) will hatch as a general rule, as low as 37 per cent and as high as 58 per cent have been found in different years (McClure 1941).

Table 42.—Productivity in Mourning Doves

State	Nests		Broods		Reference
	Number Studied	Per Cent Successful	Number Studied	Mean No. of Young	
Alabama	592	52			Pearson & Moore (1939)
Tennessee	235	52	122	1.74	Monk (1949)
Oklahoma	141	43	61	1.7	Nice (1923)
Iowa	3878	48		1.82	McClure (1941; 1943, p. 385)
Nebraska	385	48			McClure (1946)

S. H. Low (1935) has published a preliminary report on the survival of unaged birds banded by the Austin Ornithological Research Station on Cape Cod, Mass. Four years of recapture work, he reported, suggested a trend of survival reaching zero about the ninth year (? after banding). A recalculation of the data (table 43) indicates that these birds disappeared at a mean rate of about 40 per cent per year. More recently, O. L. Austin, Jr. (1951) has summarized 20 years of data on mourning doves at this station. For 269 adult birds, the mean mortality rate was 52 per cent per year; for 105 young birds, the first-year mortality rate was 75 per cent.

Banding work in North America

From 1926 to 1941 inclusive, 100 banders ringed 9929 juvenile doves; this banding total yielded 371 recoveries (3.7 per cent). Important banders of young birds in this period were E. C. Anderson (129) in South Dakota, O. L. Austin and associates (428) in Massachusetts, F. W. George (243) in South Dakota, J. W. Kistler (535) in North Carolina, F. E. and C. C. Ludwig (454) in Michigan, J. A. Neff (1487) in California, A. M. Pearson and H. S. Peters (568) in Alabama, E. Preston (147) in North Dakota, "T. G. Scott" (1551) in Iowa, C. Stannard (1869) in Arizona, and I. Sturgis (287) in Missouri. Stannard obtained 63 recoveries up to 1946, Neff 47, and Scott 63. I presume that the banding work credited to Scott in the Fish and Wildlife Service files was largely carried out by H. E. McClure (see above).

Table 43.—Disappearance of Some Massachusetts Mourning Doves

Unaged birds banded at the Austin Ornithological Research Station
(after S. H. Low 1935)

Symbols...	l_x Number Surviving	l_x Surviving	?d _x Per Cent Disappearing Between Years	?q _x Mean Rate of Disappearance
End of 1 year	81 out of 519	15.6%	8.1%	
End of 2 years	27 out of 359	7.5%	2.1%	
End of 3 years	10 out of 184	5.4%	1.3%	
End of 4 years	3 out of 74	4.1%		
3-year Totals and Mean		28.5%	11.5%	40%

Characteristics of the sample studied

Most of the recovery reports of mourning doves emanate from hunters, their monthly peak occurring in September. In order to get the effects of this early mortality into a life table, I used September 1 as a starting date. Among the 319 recoveries of mourning doves banded as juveniles that I studied at Patuxent Research Refuge, only 8 per cent had been banded in September. This agrees rather well with a graph of monthly nests for Alabama published by Moore and Pearson (1939). Apparently only a minor fraction of the continental population receives no consideration when a life table for this species is set up with the first age interval starting September 1.

Abridged life tables

The oldest mourning dove that I encountered among records of juvenile-banded birds was 36-326405, which was banded by H. S. Peters, at Auburn, Ala., on July 6, 1936, and later reported shot in Barbour County, Ala., according to a letter of W. S. Childs dated December 20, 1945. Because this report lacked a definite recovery date, I did not use it in the life tables that follow. The next oldest bird had been reported in its sixth year of life.

Table 44.—Abridged Life Table for Juvenile-Banded Mourning Doves

Based on 286 birds reported shot and 11 birds found dead. Original dates of banding extended from 1926 to 1940. Each age interval starts September 1.

Age Intervals in Years	0-1	1-2	2-3	3-4	4-5	5-6	Total
Number reported dead	191	63	17	18	3	5	297
Alive at start	297	106	43	26	8	5	485
Mort. rate (per cent per year)	64	1	56	1			

A preliminary life table for mourning doves was first compiled for 297 juvenile birds banded from 1926 to 1940 inclusive in the months of March to August inclusive. The results (table 44) indicated a first-year mortality rate of 64 per cent and a mean adult mortality rate of 56 per cent per year.

This table was next checked by using 308 birds banded as juveniles from 1926 up through 1941 and expressing the results as birds reported dead per 10,000 banded. This abridged life table (not shown here) yielded a 62 per cent first-year mortality rate and a mean of 58 per cent per year for adults.

A final check on the mortality rate for adults was obtained by analyzing a sample of 263 unaged birds banded from 1926 to 1937 inclusive. With each year starting January 1, the mean mortality rate over a 9-year span of life was 58 per cent (table 45). This particular sample was not checked against the banders' schedules, but it does convince one that the mean mortality rate for adult mourning doves has been close to 56-58 per cent per year.

Table 45.—Survival in Mourning Doves Unaged at the Time of Banding

Each year starts January 1; birds banded 1926-37; recoveries involve birds reported shot plus a small number found dead.

Years after Banding	1	2	3	4	5	6	7	8	9	Total
Number dead	146	72	28	14	0	1	0	1	1	263
Alive at start of each year	263	117	45	17	3	3	2	2	1	453
Mortality rate (per cent per year)	56	+	62	+						58

Age ratios and productivity

In a sample of about 400 mourning doves taken by pass shooting in New Mexico, Leopold (1921) found an age ratio of about 1 young to 1 adult. He pointed out that, although this ratio could hardly be affected by juvenile vulnerability to the gun, it might be distorted by age-group differences in migratory behavior (a phenomenon still unproven in this species). In contrast to this estimate that the population doubles itself by autumn, McClure (1942, 1943) has concluded that the breeding population trebles itself in Cass County, Iowa. The age ratio implied in table 43, 1.6 young per adult as of September 1 (that is, $297 \div 188 = 1.58$), is intermediate between these estimates. It is also identical to that reported for 1162 doves taken by Texas hunters (Swank 1950).

If successful broods elsewhere in the country are similar to the 1.82 young per successful nest found by McClure (1941), it would take close to 2 broods per year by each pair to balance the life-table populations examined in this study ($[2 \times 1.58] \div 1.82 = 1.8$).

McClure (1941, 1942, 1943) has given a wealth of interesting data on the productivity of mourning doves, although Nice (1943) has challenged his population analyses. McClure (1943) reports that nesting attempts averaged from 4.6 to 5.4 per pair in different years (1943, p. 384). He also gives 2.4 and 3.0 as the mean number of successful broods per pair during his best two years of observation. Multiplied by 1.82 young per successful nest, these last two values could mean age ratios of the order of 5.5 - 6.4 young per adult at the time the young leave the nest. It is impossible, of course, to convert such productivity data to precise age ratios because the nesting of mourning doves extends over a long period during which mortality is constantly occurring. It is difficult to believe, however, that age ratios of this order would shrink to something approaching 1.6 young per adult by September or October.

Population dynamics

Length of nesting season.—Some hint of the regional variations possible in mourning dove production is found in a review of the nesting activity reported thus far for the various parts of the United States (table 46). Other (smaller) samples reported on by Gander (1927) and by Grinnell, Bryant, and Storer (1918, pp. 594-596) show a nesting season in California lasting from January to December; or (more properly?) from December to October. This latter period more closely approximates the time of enlarged testes size reported for 317 Alabama birds by Pearson and Rosene (1938). It is not yet clear if the length of the nesting period varies with the mean number of broods raised by pairs that start the breeding season. Since nest building, laying, incubation and fledging typically cover 33 days (Pearson and Moore 1939), doves in the southern states could raise more broods than those in the northern states. There is no evidence yet available that they do so.

The monthly frequencies of nesting activity in table 46 indeed raise more questions than they perhaps answer at this time. What, for instance, is the meaning of the flat-type curves of nests found and broods fledged in Tennessee? One is tempted to infer that these reflect the very high average numbers of nesting attempts and successful broods reported by McClure (1943); but if this is true, why is McClure's own activity index so different?

On the other hand, the distribution of 319 banding dates in the Fish and Wildlife Service files is quite similar to that of the activity index set up by McClure (1943) for Cass County, Iowa. One should notice in the former that 70 per cent of the young were banded before August and 92 per cent before September. It seems likely that more instructive sets of statistics along these lines could be assembled by tabulating not merely recoveries in the banding files (as I did) but also the numbers of nestlings actually banded in various parts of the country.

Table 46.--Monthly Nesting Activity in the Mourning Dove

Each month's activity is expressed here as a percentage of the season's total. Statistics for Alabama were read off from a graph and should be taken as approximations.

Month	Alabama Estimated % of 592 Functional Nests 1/	Tennessee Per cent of Nests Found	Oklahoma Per cent of Broods Fledging	Iowa Per cent of Found in 1920	Canada & U. S. Per cent of 319 Young Banded	Texas Frequency of Hatching Dates of Juvenile Birds Bagged in 1949
March	3	5	-	0 ^{2/}	0.1	0.6
April	10	20	5	12	2	0.9
May	24	21	21	30	16	16
June	24	14	20	23	26	28
July	18	20	18	19	23	30
August	14	20	18	12	20	22
September	7	0.4	17	4	12	8
October	1	-	-	0 ^{2/}	1.2	-
Source	Pearson and Moore (1939)	Monk (1949)	Nice (1923)	McClure (1942)	U. S. Banding Files	Swank (1950)

1/ estimated from a graph published by the authors

2/ nests were found for these months during other years

By weight analyses Moore and Pearson (1941) have shown that very young birds constitute a sizable fraction of the mourning doves taken by hunters in Alabama. The September-October kill in that State is thus directed heavily upon the highly vulnerable late-hatched young. If we can say with certainty what fraction of the dove production comes off in each month of the season, it may be eventually possible to ascertain the relative proportions that early and late production contributes to the hunter's bag. At the present time, the life tables derived from banding data do not demonstrate--on a continental scale at least--a marked vulnerability of young birds to the gun. This may be later clarified when we know what fraction of the dove population is taken by hunters.

Mean number of broods raised.--It seems impossible with the data at hand to settle the interesting question of the mean number of broods raised by mourning doves that start each nesting season. There are virtually no published observations on marked adults observed throughout the breeding season. Highly circumstantial evidence is frequently published on the maximum number of broods raised in one year by (unmarked) pairs that consecutively use the same nest site. Records of a few pairs that raise four such broods do not imply, however, that all pairs raise four broods.

Thus if all the mourning doves in a region made four nesting attempts, and a 50 per cent nesting success occurred at random throughout the population, it can be shown¹ that 6.25 per cent of the birds would tend to raise four broods, 25 per cent three broods, 37.5 per cent two broods, 25 per cent only one brood, and 6.25 per cent no young at all. These calculations do not take into account adult mortality; they do yield a mean of two broods per pair.

Similarly, if all the doves in a region made five nesting attempts, and a 50 per cent nesting success occurred at random throughout the population, 3.1 per cent would tend to raise five broods, 15.6 per cent four broods, 31.2 per cent three broods, 31.2 per cent two broods, 15.6 per cent one brood, and 3.1 per cent no young at all. These calculations again do not consider adult mortality; they yield a mean of 2.5 broods per pair alive at the start of the nesting season.

Adult mortality should lower the mean number of broods raised by pairs that start the breeding season; its net effect should be to decrease the number of broods raised each month (exactly as Monk's brood data illustrate). Monthly variations in nesting success should, at least for some months, constitute an even more important variable, but of the operation of this factor, we know virtually nothing at this time.

¹by expanding the binomial $(a + b)^4$ where a = nesting success and b = nesting failure

Mortality and survival rates.—Over a 3-year retrapping period, S. H. Low got a much higher survival rate (60 per cent per year) on Cape Cod, than I calculated for doves (42 per cent) in this study. There is no bias in his work that I can detect, and aside from sampling limitations his result must be accepted as indicative of how widely survival rates may differ when calculated for a real population and for the theoretical ones examined in my own study. Low's results imply that, during the period he was retrapping, mourning dove populations on Cape Cod required an age ratio of only 0.67 young per adult to keep them stable. There is perhaps some implication that this species was locally increasing at the time of Low's study. Austin's recent (1951) calculation of a mean mortality rate of 52 per cent per year for adult doves on Cape Cod is much closer to the results of my own study. This first-year mortality rate of 75 per cent is notably higher.

Among the disappointments associated with my own work on doves was the impossibility of calculating mortality rates for northern and southern portions of the mourning dove population. This must clearly wait until more data are available. The work analyzed here also fails to give any clue as to the actual extent of mortality encountered by young birds fledging after September 1. One possible approach to this problem perhaps could be undertaken by a study of recovery rates with particular reference to reports of banded birds turned in by hunters.

Summary

Banding work on 9929 juvenile mourning doves has yielded recoveries of the order of 3.7 per cent, most of the reports coming from hunters. In this species, about 50 per cent of active nests hatch, each with 1.7 - 1.8 young. First-year mortality rates for young birds banded and alive on September 1 have run about 62-64 per cent, the mean adult rate being close to 56-58 per cent per year.

Dates of banding for 318 young in the Fish and Wildlife Service recovery files closely approximate the monthly frequency of hatching dates estimated for juvenile birds bagged in Texas during the fall of 1949 as well as the seasonal spread of daily nesting activity calculated for Cass County, Iowa, by McClure, 18 per cent having been marked by June 1, 46 per cent by July 1, 71 per cent by August 1 and 53 per cent by Sept. 1; these suggest that a minor fraction (hatching after September 1 and amounting to perhaps 10 per cent) of the juveniles were excluded from this study. For at least this section of the population, an age ratio of only 1.6 per adult as of September 1 seems necessary on the average to keep mourning dove populations in balance.

Chapter X.—Order Strigiformes: Owls (Family Tytonidae:
Barn Owls)

Barn Owl

Literature on Productivity and Survival

The number of young in broods of Tyto alba was found by F. N. Gallup (1949) to average 4.2 in 87 cases at Escondido, Calif. The banding files record a nestling banded June 25, 1929, at Horsham, Pa., and captured while brooding 4 eggs at Staten Island, N.Y., May 2, 1930, less than 11 months later. In a British survey of 214 nests, the mean clutch was 3.8 eggs, 3.0 hatching and 2.8 young surviving to leave the nest (Blaker 1933). Schifferli (1949) reports that in Switzerland, egg clutches average about 5.4, broods about 4.6, and that mortality rates run 76 per cent for the first year of life (from time of banding) and 57 per cent per year for adults.

Banding Work in North America

Among 230 recoveries of both adult and nestling-banded birds, 92 originated in California, 42 in Ohio, 17 in Massachusetts, and 16 in Pennsylvania; the rest were scattered among 17 states. To obtain 143 recoveries of juvenile-banded barn owls, 48 banders ringed 901 birds. About 587 other barn owls (including juveniles) were also banded, but no recoveries on these birds were recorded. The principal banders were F. N. Gallup (279 banded 1926-41, 24 recoveries) and J. G. Peterson (109 banded, 14 recovered); both men worked in California. Among the recoveries of juvenile-banded birds were 49 found dead, 44 shot, 19 captured, 11 caught in steel traps, 7 found injured, and 5 killed by autos. For 8, there was no recovery information.

Characteristics of the Sample Studied

Two nestlings were banded in January (Illinois and Texas), 2 in March (California and Florida), 4 in September, 5 in October, and 5 in November. Eighty-six per cent of the nestlings were ringed from April to July inclusive. To take advantage of the full sample, I started the life-table analyses for this species as of the date each bird was banded. In banding work with colonial species this would certainly be poor technique (since dead birds found in colonies do not involve a random type of recovery); in noncolonial species, very few recoveries are reported immediately after the birds leave the nest (so that dating of this kind biases first-year recoveries in the opposite direction). In the barn owl bandings, this hiatus of reports was not evident (table 47), and I concluded that such dating of the barn owl year gives a reasonable set of workable data.

Table 47.—Monthly Distribution of Barn Owl Recovery Reports

This breakdown is restricted to birds banded as juveniles through 1941 but includes recoveries of birds reported both dead and alive as well as those with no information as to method of capture up to 1946.

Year Recovered after Banding	Approximate Number of Months Recovered after Banding											Total	
	0	1	2	3	4	5	6	7	8	9	10		
First year	8	10	5	9	9	9	5	8	12	6	3	4	88
Later years	5	8	1	5	7	7	3	6	4	10	0	3	59

As table 48 shows, the age ratio in barn owl recoveries is about 60 per cent juveniles to 40 per cent adults. The percentage of adults should increase slightly as additional birds are reported. The percentage of young in the "found dead" sample and in the sample of birds reported shot do not differ significantly from this 60-40 ratio. The similarity in age ratios between birds reported dead and those captured, caught, or found injured implies that the individuals in this latter category are representative of those dying in the population.

Table 48.—Age Ratios in Barn Owl Recoveries

Juvenile-banded birds as in table 47 except that only specific methods of recovery were tabulated. Based on birds banded through 1941, this table includes recoveries received through 1946. Some additional reports of birds recovered as adults should slightly decrease the percentage recovered as juveniles and make the data comparable to that found in a life table.

How Recovered	When Recovered			% Young
	As Young	As Adult	Total	
Found dead	24	25	49	49
Shot	32	12	44	73
Killed by auto	3	2	5	-
Subtotal	59	39	98	60
"Captured"	14	5	19	-
Caught in steel trap	4	7	11	-
Found injured	4	3	7	-
Subtotal	22	15	37	59

Irving Kassoy has pointed out to me in a letter that this sample presumably involves both migratory and nonmigratory populations. With so many of the recoveries emanating from California at

the present time, it seems likely that the survival rates calculated here will refer—for the most part—to nonmigrants.

Abridged Life Table

An abridged life table for barn owls is given in table 49, where a mortality series is computed as the number reported dead per 1000 banded birds available for each age interval. The number of banded birds was ascertained by taking the recovery cards in the Fish and Wildlife Service files and tabulating the numbers that the successful cooperators actually banded. The number banded by unsuccessful banders could not be ascertained without a prolonged and exhausting survey. As a check on possible discrepancies introduced by this method, a second life table was constructed using Lack's (1943a) method on birds banded up to 1935. For 55 birds found dead or reported shot, the mean mortality rate was 42 per cent per year (in contrast to 40 per cent in table 49). On the theory that captured barn owls are equivalent to dead ones, another table involving 80 recoveries of all kinds was constructed using Lack's method on birds banded to 1935. This again yielded a mean mortality rate of 42 per cent for all age intervals. Both these tables (which are not shown here) had the same first-year mortality rate (51 per cent) and nearly identical mean adult mortality rates (35 and 37 per cent per year respectively).

The adult mortality rate in table 49 was next checked by computing the mean mortality rate for 33 birds banded as adults up to 1935. Using recoveries of all types but excluding birds recovered within one week after banding, this new calculation yielded a mean rate of 34 per cent per year. Excluding 14 adults that were recovered within a year after banding dropped the sample to 19 birds and the mean mortality rate to 30 per cent per year.

Age Ratios and Productivity

It seems certain that Barn Owls breed when one year old. The 172 adults in table 49 (column l'_{x_1}) could keep the population stable if each pair raised 1.33 young per year. This is so far below the 4.2 young observed in successful nests by Gallup (1949) in California that the discrepancy calls for some explanation. Several possibilities require comment:

- (1) That sampling errors occur in the life table. It is certain that these exist but I fail to see how they could exaggerate and distort the age ratios and required productivity to the extent described here.
- (2) That the construction of a life table (no. 49), starting as of the date of banding, is false. A review of table 47 will convince one that there is at least no hiatus of banding recoveries in the weeks or months following the banding date. There are

Table 49.—An Abridged Life Table for Barn Owls

Birds banded as nestlings. The first age interval starts as of date of banding. Columns d'_x and l'_x were calculated to two decimal places and then rounded off. This has left minor discrepancies in the survival series, which represents the number alive at the start of each age interval and is computed directly from the mortality series. The mortality series represents the number recovered dead per 1000 banded birds available at each age interval.

(1) Age Interval in Years	(d) No. Shot or Found	(2) Banded Birds Available	(d'_x) Mortality Series 1000 [d_x / (2)]	(l'_x) Survival Series	(q_x) Mortality Rate (per cent per year)
0-1	59	901	65.5	113.4	58
1-2	13	901	14.4	47.9	1
2-3	8	901	8.9	33.5	1
3-4	7	901	7.8	24.6	1
4-5	4	901	4.4	16.8	28
5-6	1	834	1.2	12.4	1
6-7	1	732	1.4	11.2	1
7-8	2	588	3.4	9.8	1
8-9	1	492	2.0	6.4	1
9-10	1	479	2.1	4.4	1
10-11	1	437	2.3	2.3	1
Total and Mean	-		113.4	282.7	40

undoubtedly mathematical fine points that are beyond my comprehension in this connection, but it is hard to believe that unrecorded juvenile mortality is creating an important bias here. Cannibalism among the young is, however, a phenomenon that would leave no trace in banding records. It is known to occur in this species, but its extent remains to be quantitatively determined.

(3) That Gallup's productivity data are atypical of the rest of the continent. To check this, the Fish and Wildlife Service files were studied to determine what brood sizes were definitely mentioned by banders in their reports. These compare to Gallup's data as follows:

Size of Brood	1	2	3	4	5	6	7	Total No. Broods
F. N. Gallup	3	9	11	28	18	14	4	87
Other banders	2	5	6	9	7	6	1	36

The available evidence certainly indicates that 4 can be regarded as the typical brood size for this species in North America.

(4) That the discrepancy between the field data and the life-table data is the result of a comparison between successful pairs and the combination of successful plus unsuccessful pairs. This seems to me to be an hypothesis that is tenable at this time. It implies, however, that only about 30 per cent of the females succeed in raising 4 young to the banding stage.

Population Dynamics

The North American data on the number of young Barn Owls in the nest (4.2 by Gallup in California, 4.0 for broods noted in the U. S. banding files) agree rather well with the 4.6 calculated by Schifferli for Switzerland. Against these the British data published by Blaker (1933)--3.8 eggs, 3.0 hatching, 2.8 young leaving the nest--offer a remarkable contrast. At least three hypotheses may be offered to explain this discrepancy: (1) that the British data were collected in a relatively short period and are representative of a low point in the barn owl's "cycle" of productivity; (2) that British barn owls differ from Swiss barn owls in their population dynamics in somewhat the same way as Lack and Schifferli (1948) found the starlings of these two countries do; and (3) that some as-yet-unknown bias exists in the manner that Blaker's inquiry operated. These interesting questions can best be settled by a study of brood sizes reported in the British banding files over a period of years and perhaps also by calculations of mortality rates in the British barn owl population.

Of equal interest is the striking discrepancy in mortality rates now available for Swiss and American populations of this species: for birds in their first year of life (from the time of banding), 76 per cent calculated by Schifferli (1949) and 51-58 per cent in my study; 57 per cent per year for adult Swiss birds, and about 28-37 per cent for American ones.

No convincing explanation is offered in this study for the apparent discrepancy between productivity in the American barn owl and subadult and adult mortality rates. Although the mortality rates calculated here are derived from small samples, it seems certain that they are low among the adult birds and probably of the order of 30 per cent per year. The high productivity of the successful females must be counterbalanced by some major phenomenon in the life history and ecology of this species. This possibility can be re-assessed when a larger sample of banded birds is available for study. At the moment, I have no solution to the problem to offer.

Summary

Nestling barn owls have been banded in North America in every month except February and December, 86 per cent of the banded nestlings being ringed from April to July inclusive. Recoveries of the young birds are reported throughout the 12 months following banding. Small-sample analyses yielded first-year mortality rates (from the date of banding) of 51 per cent per year (2 samples) to

58 per cent (98 birds). For adults, the mean annual mortality rates were estimated to be about 28-37 per cent. These are considerably lower than rates computed by Schifferli (1949) for Swiss birds.

No convincing explanation was offered to account for the high productivity of successful females (4 young per brood) and the low mortality rates here encountered. The oldest bird among 98 records had reached 10 years of age.

Family Strigidae (Other Owls)

Great Horned Owl

Literature on Productivity and Survival

The average number of eggs laid by Bubo virginianus is said to fluctuate regionally and perhaps annually (Bent 1939: 302, 329). According to Baumgartner (1938), the usual number is 2, full sets of one being frequently found in Florida, and sets of 5 to 6 occasionally reported from central and western North America.

Nothing appears to have been published on the age at which this species begins to breed. When one considers the great size of these birds, it is possible that they do not nest until at least 2 years old.

Banding Work

Great horned owls had been banded and recovered in 35 different provinces and states up to July 30, 1946. The largest numbers of recoveries (among 162 records of adults and young initially examined) were from Alberta (20), Michigan (14), and Ohio (10). Among the banders, those with the largest numbers banded were C. R. Berry of Wyoming (57), R. H. Pough and cooperators (56), and George Wagner and cooperators (34). From 1926 to 1941 (inclusive) 55 banders, ringing 476 nestlings, got 113 recoveries. This is a recovery rate of 23 per cent. About 400 more horned owls were banded by other persons who either got no recoveries whatever or who worked with adult birds.

Characteristics of the Sample

In spite of the smallness of the sample, horned owl recoveries in the aggregate (table 50) display something of the autumnal frequency peaks found in so many other species, but the monthly distribution of mortality reports is rather well spread out throughout the year. The samples are too small to show significant differences between types of recovery, but there is some indication that the proportion of birds shot in the fall is about the same for young as well as adults. In constructing some preliminary life tables for this species, I used all 3 types of recovery. All the owls in these samples were banded as nestlings. Use of captured birds in the life tables is carried out with the assumption that capture in this species is virtually synonymous with death.

Abridged Life Table

A preliminary life table for subadult and adult great horned owls is given in table 51. Because the annual mortality rates of 51 (for juveniles) and 23 per cent (for adults) are based on only 58 birds, the results will have to be confirmed by subsequent analysis of a larger

Table 50.—Monthly Variation in Reported Recoveries of Great Horned Owls

The birds were banded as nestlings from 1926 to 1942.

STT

When Recovered	How Recovered	Month Reported Recovered												Total
		VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	
First year	Shot	1	5	4	4	3	2	2	1	1	2	3	-	28
	Found dead	-	-	2	1	-	-	-	1	-	1	1	-	6
	Captured	-	2	1	2	1	1	2	-	2	1	-	2	14
Subtotal		1	7	7	7	4	3	4	2	3	4	4	2	48
Later years	Shot	1	3	6	4	1	1	1	2	-	2	2	-	23
	Found dead	1	-	-	-	1	-	-	-	2	-	-	1	5
	Captured	1	-	3	-	1	-	3	-	-	1	1	-	10
Subtotal		3	3	9	4	3	1	4	2	2	3	3	1	38
Total		4	10	16	11	7	4	8	4	5	7	7	3	86

Table 51.—A Preliminary Life Table for Great Horned Owls

Based on nestlings banded from 1926 to 1941 inclusive, each year starting September 1. The number of banded birds available was ascertained by taking the recovery cards and checking them against the banders' original reports. The number banded by persons who got no recoveries was not determined. Its inclusion in this table would lower the values in columns l'_x and d'_x , but would not seriously alter the mortality rates obtained here. The mortality series in this table represents the number reported dead per 1000 banded birds available. From it, the survival series is derived after the method of Lack.

(1) Age Interval in Years	(d) No. Shot or Found Dead	(2) Banded Birds Available	(d') Mortality Series 1000 [$d_x \div (2)$]	(l') Survival Series	(q) Mortality Rate (per cent per year)
0-1	33	478	69.0	135.9	51
1-2	9	478	18.8	66.9	
2-3	8	478	16.7	48.1	
3-4	3	478	6.3	31.4	
4-5	1	478	2.1	25.1	
5-6	1	398	2.5	23.0	
6-7	0	337	-	20.5	
7-8	1	222	4.5	20.5	23
8-9	0	178	-	16.0	
9-10	1	162	6.2	16.0	
10-11	0	128	-	9.8	
11-12	0	112	-	9.8	
12-13	1	102	9.8	9.8	
Total and Mean			135.8	432.8	31

sample. A second criticism arises from the fact that not all banded birds available for study were actually counted by me in the Fish and Wildlife Service files. (Time did not permit me to determine the number of horned owls banded by persons who obtained no recoveries whatsoever.) To test this criticism, I set up a small table of 20 birds banded prior to 1933 and later shot or reported as found dead. Using Lack's method, these 20 yielded a mortality rate of 50 per cent for the first year of life and a mean rate of 26 per cent per year for adults. This result at least does not discredit the method used in table 51; it also carries the implication that the sampling errors in table 51 may be less than originally suspected.

In an effort to obtain further clues to at least the adult mortality rate for this species, 38 recoveries of horned owls banded as adults were examined. Nineteen of these were recovered within one month after banding, and most of these 19 were within one week. It seems obvious that the original capture of these adults either doomed many of

them to early death or was the result of a circumstance that had already determined the fate of these individuals. Thus, injuries sustained from pole traps or gun shot would fulfill these conditions and bias the sample for a longevity study. Excluding these 19, other adults were recovered as follows:

<u>When Recovered</u>	<u>Number Recovered</u>
Same year	11
1 year later	3
2 years later	1
3 years later	2
4 years later	1
5 years later	0
6 years later	1

I interpret this mortality series as probably biased for birds recovered within one year of capture. The fact that 30 out of 38 died within one year after banding should be noticed in connection with the assumption stated earlier in this chapter that captured horned owls can usually be regarded as dead ones. The 8 birds shot one or more years later appear to represent a reasonable confirmation of the low adult mortality rate for adults obtained in the life table above. This seems to be as far as we can go at the present time.

Age Ratios and Productivity

If this species breeds at the age of 2 years, a hypothetical population such as that given in column $1'_{x}$ of table 51 could remain stable if each pair raised 1.2 young successfully to September 1. This hypothesis is hard to verify at the present time.

If all horned owls do breed at the end of one year, population balance in this species would be achieved either by a fairly high percentage of nesting failures or very low early survival of the young. The first of these alternatives seem possible. Fitch (1940) has shown that 3 nests out of 5 on a California study area failed because of weather, predation, and unsanitary nest conditions; a much more intensive nesting study or an extensive inquiry is still needed to settle this interesting question.

Population Dynamics

The possible existence of a continental gradient in the mean size of clutches of great horned owls seems to be suggested in the ornithological literature. When sufficiently large samples of banding recoveries are available, regional subadult and adult survival rates may have to be correlated with regional variations in the mean number of eggs and young produced. The small samples assembled in the present study originated mostly from banding work in the northern part of the United States and the southern part of Canada.

It seems certain that in this species we have encountered a rather low adult mortality rate. The monthly distribution of the banding recoveries is well spread out throughout the year. This implies that the first-year mortality rate calculated in this study is not biased by a heavy preponderance of shooting reports in the fall of the year, although the size of the sample does not permit one to regard the result with confidence.

Both the horned owl and the blue jay (which follows in the next chapter) present difficult problems to a field investigator interested in obtaining statistically significant data on average productivity. Nesting information for both species might well be gathered by an organized inquiry using a questionnaire.

Summary

Three separate analyses of horned owl banding data indicate that the mean adult mortality rate is of the order of 20-25 per cent. The samples examined were all quite small, and the estimate obtained here must be regarded as an approximation. A first-year mortality rate of 51 per cent, obtained for 58 birds banded as nestlings, is obviously subject to sampling error and not easy to verify at this time.

Mortality reports of 86 banded great horned owls were rather well distributed throughout the year. The oldest bird thus far recovered had reached age interval 12-13.

Chapter XI.—Order Passeriformes: Perching Birds (Family Corvidae: Crows and Jays)

Blue Jay

Literature on Productivity and Survival

Although Cyanocitta cristata is one of the commonest breeding birds in eastern North America, no statistics have been published on the mean number of eggs or the mean number of young. Tyler (1946) says that the northern race bromia "ordinarily lays four or five eggs." According to D. J. Nicholson (Howell 1932), first sets of the southern race cristata nearly always consist of 4 eggs, second sets 3 or 4, third sets nearly always 3. These statistics presumably apply to renestings following loss of eggs.

Birds that were one year old have been observed as pairs and in the act of copulation (M. B. Hickey, verbal communication). At least in southern Michigan, this species is normally single-brooded (ibid.).

Banding Work in North America

From 1926 to 1941 inclusive, banders who ringed over 100 juveniles each were: D. M. Morrison, M. Clow, E. A. McIlhenny, W. M. Davidson, F. M. Cutler, J. A. Gillespie, C. Everett, C. W. Allison, J. A. Laughlin, G. Gill, E. C. Hoffman, and P. H. Oppmann. The 114 banders who obtained 257 recoveries of juvenile-banded birds ringed a total of 4547 birds for a recovery rate of 5.8 per cent.

Characteristics of the Samples Studied

The banding of young blue jays was spread over 5 months; May, 6 per cent; June, 21 per cent; July, 33 per cent; August, 32 per cent; and September, 8 per cent. This last month's work was not used in this study, partly to retain September 1 as a starting date in life-table analysis and partly to avoid possible errors in age identification at the time the birds were banded.

The monthly distribution of the more prevalent types of recovery is illustrated in table 52. Several interesting aspects deserve mention. Among the birds found dead, we encounter—for the first time in this study—a spring peak in the frequency of reports that is higher than the autumnal peak. The cause of this was not determined with certainty. Among 152 blue jays unaged at the time of banding, 4 were reported as brought in by dogs, 5 were alleged to have been killed by hawks or owls, 8 were said to have drowned (mostly in barrels), 16 were reported as killed by striking wires, 18 were found dead after storms (usually blizzards), 31 were said to have been killed by automobiles, and 70 were reported to have been killed by cats. Eight hundred and eighty-six others unaged at the time of banding were said to have died from unknown causes.

The peak of occurrence for 495 of these (recovered after December 31 of the year in which they were banded) was found to coincide closely with that of the juvenile-banded birds. Whatever the actual causes of mortality may be, their peak occurrence in the breeding season seems important.

If the age ratio of the birds dying each year between September 1 and August 31 in blue jay populations is 0.54 young to 1 adult (as in the birds found dead in table 52), samples of 49 would show an even age ratio about once in 20 times. It seems best, therefore, to regard the 49 birds shot (table 52) as biased in favor of juveniles and to use them only with caution in an abridged life table.

Table 52.—Monthly Variation in Recoveries of Banded Blue Jays

Based on birds banded as young during the months of May, June, July, and August, from 1923 to 1941 inclusive. Some of the recovery dates may include slight clerical errors but the seasonal trends should be accurate within the limits of the size of each sample. Age ratios implied in this table are subject to additional reports of adult birds being recovered after 1946.

Age Reported	Frequency of Reports by Months (September to August)												Total
	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	
<u>Found dead</u>													
First year	8	5	3	4	4	2	3	2	10	7	3	3	54
Adult	8	5	8	2	10	6	6	11	15	14	9	7	101
Total	16	10	11	6	14	8	9	13	25	21	12	10	155
<u>Shot</u>													
First year	3	6	0	4	3	0	1	0	2	0	3	2	24
Adult	4	5	2	1	2	1	0	0	0	8	2	0	25
Total	7	11	2	5	5	1	1	0	2	8	5	2	49

Abridged Life Tables

In order to avoid any possibility of substandard bands influencing the mortality statistics, banding operations from 1923 to 1925 inclusive were not used in constructing life tables. Six such tables were set up, and the results are summarized in table 53. Here for the first time we encounter a first-year mortality rate that does not seem to be higher than the mean adult mortality rate. Lack (1946b) has shown that the higher mortality rates for young songbirds drop to those of the adult birds by January 1. The recovery reports of blue jays found dead are more frequent in the spring than in the autumn (table 52). We apparently are faced here with a situation that was theoretically explored in Chapter III, table 13. There is no proof that the first-year mortality rate (September 1—August 31) for blue jays is higher

than the mean adult mortality rate. There is, however, some reason to believe that--if such existed in this species--it would not necessarily be detectable in the mortality data analyzed here. The sample of birds shot, when added to the birds found dead, appears to be too small to demonstrate what is happening to the population during the autumnal period.

Table 53.--Calculated Mortality Rates for Blue Jays

* means banded as juveniles; age intervals start as of September 1.

means unaged at time of banding; age intervals start as of January 1.

Source of Recovery	Size of Sample	Cohorts Used	Calculated Mort. Rate		Analytical Method
			1st-Year	Adult (mean)	
Found Dead	117*	1926-36	38	39	Lack (1943a)
	153*	1926-41	34	37	Per 1000 banded
	457#	1926-36	--	45	Lack (1943a)
Found Dead or Shot	150*	1926-36	41	42	Lack (1943a)
	211*	1926-41	40	40	Per 1000 banded
	636#	1926-36	--	45	Lack (1943a)

Some comment is needed on the pronounced tendency of these banding data to yield a higher mortality rate for adults in contrast to that calculated for first-year birds. This is either a band-loss effect or something actually occurring in nature. Without productivity data, it is difficult to identify the actual reason at this time. Part of the circumstantial evidence for a constant adult mortality rate in wild birds lies in the comparison of longevity in captivity. There is much evidence that, in the wild, birds attain only a fraction of the life span they achieve in captivity (Gurney 1899, Flower 1925 and 1931, Farner 1945, Marshall 1947). This situation strongly implies that senility with its presumed increase in vulnerability to predation and other environmental hazards is seldom attained by birds under natural conditions.

For the record, I should add that near Ann Arbor, Mich., my wife and I for several weeks observed a blue jay with a thin, much-worn band that was partly open and about to come off the bird's leg. We feel certain that this individual did lose its band before my wife was finally able to trap it.

Details of the uncorrected mortality data for blue jays unaged at the time of banding are given in table 54. If band loss does occur in this species, it is probable that the first four age intervals are the most accurate ones. Extension of a line through these points (figure 12) suggests that about 22 more birds might have been recovered. These would represent a band loss of about 3.4 per cent. Added to a life table they would drop the mean adult mortality rate to 42 per cent per year.

Table 54.—Survival in Blue Jays Unaged At Time of Banding

These birds were banded 1926-36. Each year in the table starts January 1.

Symbol	Part A			Part B			A + B		
	(d_x) Number Found Dead	(l_x) Alive at Start	(q_x) Mortality Rate	(d_x) Number Shot	(l_x) Alive at Start	(q_x) Mortality Rate	(d_x) Shot & Fd. Dead	(l_x) Alive at start	(q_x) Mortality Rate
0	200	457	44	73	179	41	273	636	43
1	110	257	43	49	106	—	159	363	44
2	68	147	46	25	57	—	93	204	46
3	38	79	—	18	32	—	56	111	50
4	18	41	—	9	14	49	27	55	—
5	10	23	48	2	5	—	12	28	—
6	7	13	—	3	3	—	10	16	51
7	3	6	—	0	0	—	3	6	—
8	3	3	—	0	0	—	3	3	—
Total	457	1026	44.5	179	396	45	636	1422	44.7

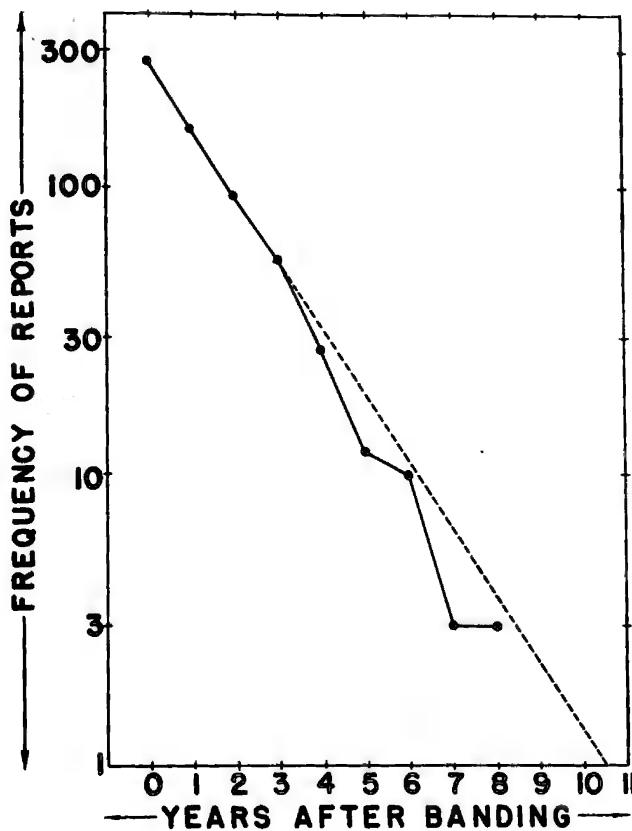


Figure 12.—Mortality in 636 Blue Jays Unaged at the Time of Banding. Solid line represents actual reports of birds shot and found dead. Broken line is the suspected mortality curve obscured by alleged band loss among the older birds or by sampling errors.

Summary

A complete lack of quantitative data on blue jay productivity currently prevents any satisfactory analyses of population dynamics in this species.

Of the blue jays said to be juvenile at the time of banding, 6 per cent were banded in May, 21 per cent in June, 33 per cent in July, 32 per cent in August, and 8 per cent in September. To obtain 257 recoveries of juvenile-banded birds, 114 banders ringed 4547 jays—a recovery rate of 5.8 per cent. Birds found dead demonstrated a mortality peak that occurred in the spring, especially in May and June. This prevented any reliable calculation of a first-year mortality rate as of September 1. The mean adult mortality rate was computed as 45 per cent per year. Band loss perhaps distorted this result slightly. The oldest blue jay noted in this study died in its tenth year of life.

PART III. IMPLICATIONS OF MORTALITY DATA, WITH SPECIAL REFERENCE TO THE MALLARD

Chapter XII.—Indices of Mortality, Hunting Pressure, and Populations

Use of Seasonal Recovery Rates in the Past

The Lincoln population index.—More familiarly known as the Lincoln Index, this represents the first attempt to use seasonal recovery rates in a statistical ratio. Lincoln (1930) suggested that if we can obtain a fairly accurate statement of the number of waterfowl killed in any one season in North America, then

$$\frac{\text{the no. of waterfowl banded}}{\text{the no. recovered in their 1st hunting season}} = \frac{\text{The no. of waterfowl in N. A.}}{\text{the no. killed by hunters}}$$

Lincoln observed that the first-season recovery rates for waterfowl in the aggregate appeared to average about 12 per cent. If the total kill by hunters was, say, 5,000,000 waterfowl, the fall population on the continent would be about 42,000,000.

The difficulties attending the application of this index have been many. One serious obstacle has been the continued lack of reliable data on the total number of waterfowl taken by hunters. Another has been the uncertainty as to the percentage of recovered bands that never are reported to the Federal Government. Estimates have been presented by Leopold (1933: 156) that this is (or has been) 50 per cent in Connecticut, 60 per cent in Arkansas, and 80 per cent in the Carolinas. McIlhenny (1934) has estimated that 50 per cent or less of recovered duck bands are unreported. More recently, Bellrose (1945) has concluded that this percentage has been only 25 per cent in Illinois in recent years. This statistic was obtained from 509 post-card replies to a questionnaire sent to 1000 randomly selected hunters. It may or may not prove to be accurate. If, among 50.9 per cent of Illinois hunters who respond to a questionnaire containing a card for reply, 75 per cent have troubled themselves to report a band, can we be sure that the other 49.1 per cent who do not return a card have a similar degree of cooperativeness in reporting bands? Their failure to reply to the questionnaire casts some doubt on their cooperativeness. Bellrose's interesting study does permit us to say that the percentage of reported bands in Illinois is somewhere between 37.5 and 75 per cent.

Recent attempts to get fairly accurate estimates of the hunting kill and detect the percentage of unreported bands hold some promise that the Lincoln index may yet be used as a check on waterfowl numbers. As Lincoln (1930) says: "The figures could only be considered as approximations, but they at least have the merit of being based on factors that appear to have a definite relationship." If the index is ever used, the seasonal recovery rate should not, I feel, be a mean value covering many years of banding. A glance at

Lincoln's data shows that, although his mean rate was 11.94 per cent, the extremes for specific years varied from 10.68 to 15.16 per cent. Lincoln has quite properly emphasized that the proximity of a banding station to an area of intensive hunting must be an important variable in the recovery rates for waterfowl banded in different regions, and that these rates undoubtedly vary according to that part of the hunting season in which the birds were banded. Recognition of the additional possibility that variations in first-season waterfowl recovery rates arise from annual differences in hunting pressure has had to await the accumulation of more banding data.

Banding index of hunting pressure.--Bellrose (1944, p. 369-370) has used first-season recovery rates as an index of the cumulative effect of federal regulations on the continental take of ducks. For black ducks in Michigan these rates dropped from 20.5 per cent in 1928-34 to 9.2 per cent for 1939-42. He also contrasts a rate of about 13 per cent for all waterfowl quoted by Phillips and Lincoln (1930) to a rate of from 5.6 to 7.5 per cent for Canadian waterfowl in 1940-1942 reported by B. W. Cartwright of Ducks Unlimited (Canada). These changes in seasonal recovery rate led Bellrose to conclude that regulations in the past ten years cut about in half the rate of kill made by hunters in the previous decade.

There are at least two possible criticisms of this method, neither of which is necessarily valid but both of which encourage skepticism: (1) We know nothing of chronological differences in the percentage of hunter cooperation in reporting bands. When hunters complain about strict regulations, are they less apt to report bands to the federal agency responsible for the regulations? (2) Are recovery rates for different banding stations so similar that these comparisons are valid? In 1939, C. J. Henry and Merrill Hammond banded 918 mallards at the Lower Souris National Wildlife Refuge, obtaining a first-season recovery rate of 15.3 per cent. During the same year S. H. Low banded 4000 mallards at the Des Lacs National Wildlife Refuge in the same state and got a seasonal recovery rate of 10.1 per cent. This difference could of course represent variation arising from differences in the date of banding, a possibility that I did not attempt to explore. Although recovery rates have yet to be correlated with mortality rates, Bellrose's (1945) use of a recovery-rate index immediately impresses one as an original intellectual contribution that has great potentialities in the study of waterfowl populations. Some of these potentialities are explored in the two sections that follow.

Regional Agreement in Seasonal Recovery Rates

Bellrose and Chase (1950) have made the interesting point that (adjusted) seasonal recovery rates have annually varied in a somewhat similar manner for two banding stations about 175 miles apart in Illinois. In table 55, I have summarized some first-season recovery rates for banding stations somewhat farther apart. No

Table 55.--First-season Recovery Rates of Mallards

Canadian birds were banded before September 1 (except as noted) and were recovered in the hunting season that followed; Illinois bandings continued through the hunting season; not included among the recoveries are birds retrapped by banders, those fatally injured in banding operations, and those caught in mammal traps.

Age	1939	1940	1941	1942	1943	1944	1945	1946	Total
CANADA 1/									
No. banded juv.	19	352	244	68	604	903	784	754	3728
No. recovered	4	39	20	8	31	83	80	72	337
Recovery rate	-	11.1	8.2	-	5.1	9.2	10.2	9.5	9.0
No. banded adult	16	313	191	58	393	681	1004	291	2947
No. recovered	1	36	4	7	27	88	103	26	292
Recovery rate	-	11.5	2.1	-	6.9	12.9	10.3	8.9	9.9
No. banded all	35	665	435	126	997	1584	1788	1045	6675
No. recovered Ages	5	75	24	15	58	171	183	98	629
Recovery rate (a)	-	11.3	5.5	11.9	5.8	10.8	10.2	9.4	9.4
rate (b)		8.9	5.7	6.4					
NORTHEASTERN ILLINOIS 2/									
Males banded juv.	-	183	116	778	1290	637	819	523	4346
No. recovered	-	16	5	68	66	67	83	40	345
Recovery rate	-	8.7	-	8.7	5.1	10.5	10.1	7.6	7.9
Males banded adult	-	84	79	350	632	330	673	333	2481
No. recovered	-	4	4	28	24	37	43	17	157
Recovery rate	-	-	-	8.0	3.8	11.2	6.4	5.1	6.3
No. banded all	-	183	312	1882	3009	1778	2287	1631	11,382
No. recovered ages 3/	-	39	16	146	152	168	198	111	830
Recovery rate	-	8.1	5.1	7.8	5.1	9.4	8.7	6.8	7.3
ILLINOIS RIVER VALLEY RECOVERY RATES 4/									
Mallard only all	2.9	6.8	2.6	5.7	-	-	-	-	-
3 species 5/ ages	1.8	5.0	1.8	3.0	-	-	-	-	-
LOWER SOURIS REFUGE, N.D. 6/									
No. banded all	918	1566	1619	-	-	-	-	-	4103
No. recovered ages	140	222	143	-	-	-	-	-	505
Recovery rate	15.3	14.2	8.8	-	-	-	-	-	12.3

1/ By Ducks Unlimited (Canada). Noted under (b) are recovery rates for unaged birds reported by B. W. Cartwright to Bellrose (1944); these rates presumably include birds banded during the hunting season.

2/ Banding work mostly by John Jedlicka for the Forest Preserve District of Cook Co., Ill.

3/ Includes females and unaged birds not shown in this table. The recovery totals differ unimportantly from those reported by Mann, Thompson, and Jedlicka (1947).

4/ From Bellrose (1944).

5/ Mallards, black ducks, and pintails banded in large numbers by the Illinois State Natural History Survey; from Bellrose (1944).

6/ Banding work by C. J. Henry and Merrill Hammond mostly during the hunting season.

compensations have been made, however, for banding that occurred during the hunting season. The higher recovery rate for Canadian-banded adults, as compared to that for Canadian-banded juveniles, should be noticed. This result is directly the reverse of the evidence of juvenile vulnerability to the gun obtained in large-scale bandings in Illinois (Mann, Thompson, and Jedlicka, 1947; Hawkins, personal communication). The lowered recovery rate for Canadian juveniles could be explained as a predation effect: if these Canadian young birds are at least as vulnerable as those banded in northeastern Illinois, we can say of the recovery rates that

$$\frac{\text{the rate for Illinois adults}}{\text{the rate for Illinois juveniles}} = \frac{\text{the rate for Canadian adults}}{\text{the expected rate for Canadian young}}$$

From table 55, it follows that

$$\frac{6.3\%}{7.9\%} = \frac{9.9\%}{x} \quad x = 12.41\%$$

Now if 12.41 is the percentage expected from (say) 100 birds at the time of banding, and 9.0 is the percentage actually obtained, then nonshooting mortality must have reduced the 100 to some new figure y at the start of the hunting season, it would appear then that

$$\frac{12.41}{100} = \frac{9.0}{y} \quad y = 73$$

In other words, decimating factors quite apart from hunting inflicted a mortality of about 27 per cent (i.e., 100 minus 73), from the time the birds were banded to the start of the hunting season. If the vulnerability of Canadian-banded juveniles is really higher than that of Illinois-banded juveniles (as I suspect), then the nonhunting mortality here computed is too low.

These computations are wholly erroneous if the Canadian banders failed to report all the adult mallards they banded. This possibility was thoroughly explored by checking the number of bands issued to the banders against the number they reported to have used. Although a number of clerical oversights were encountered, the skepticism was without basis in the present connection.

Regionally, the best agreement between fluctuating seasonal recovery rates was found in the samples for adults and for all-age groups (figures 13 and 14). The latter, of course, are larger in size, more statistically reliable, and free of the impediments of age determinations. The banding by Ducks Unlimited (Canada), being scattered through the southern parts of Alberta, Manitoba, and Saskatchewan, is more apt to be free of local mortality influences than the other samples. It is of some interest that ducks banded on a Federal refuge in North Dakota showed the highest recovery rate in these samples. The implication, of course, is that a Federal refuge does not necessarily place ducks out of reach of hunters.

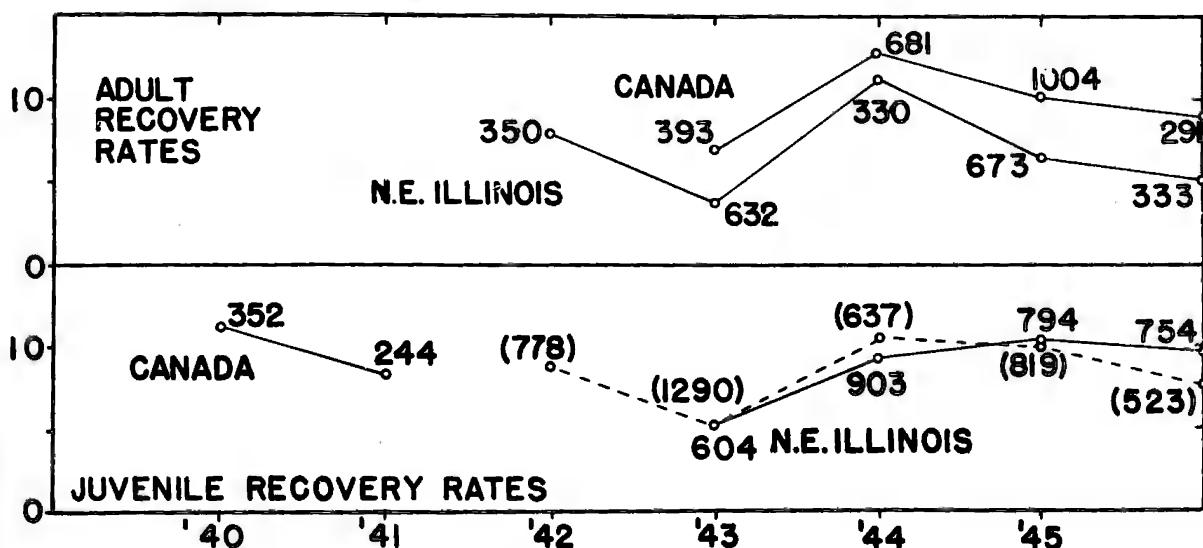
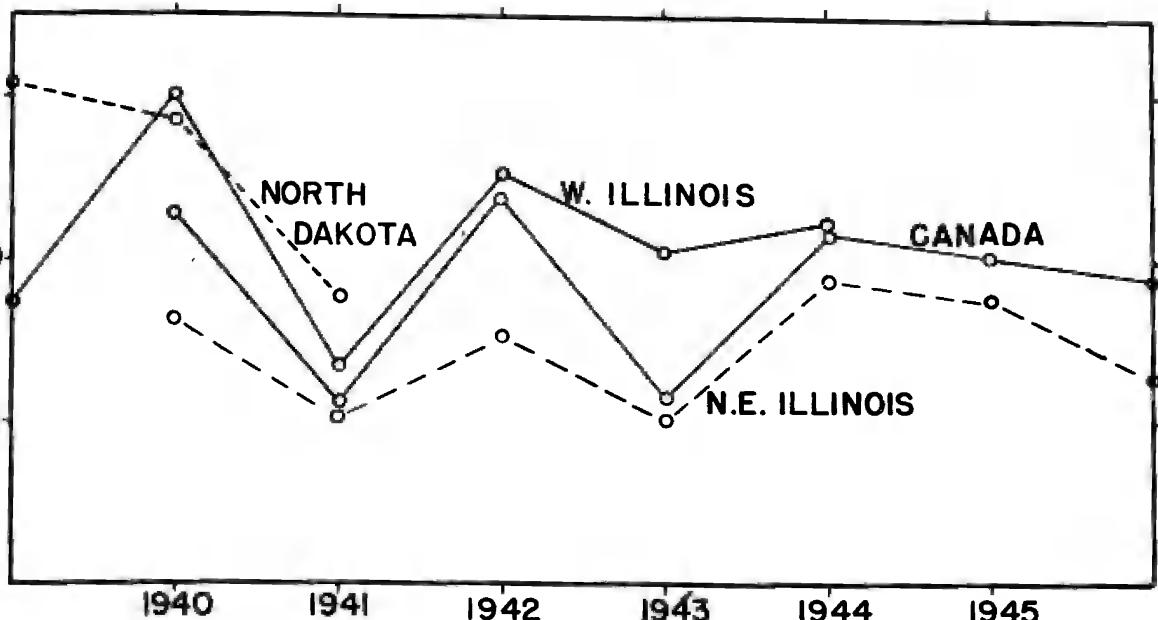


Figure 13.—Some First-season Recovery Rates for Mallards Unaged at the Time of Banding. The western Illinois data include Bellrose and Chase's (1950) adjustment to correct for the fact that the birds were banded during the hunting season.

Figure 14.—Mallard First-season Recovery Rates by Broad Age Classes. Numbers on each curve indicate the number of birds actually banded.

Elder (1946) has already shown that a state refuge can be a death trap for Canada geese. The fluctuations in rate shown here appear to have no relationship to the number of hunters or recent hunting regulations.

Because many duck-banding operations have been carried on during the course of a hunting season, Thompson and Jedlicka (1948) and Bellrose and Chase (1950) have worked out several formulas to compensate for the lapse of time between the opening date of hunting and the subsequent dates on which the ducks are banded. It is hardly fair to these fine intellectual contributions to point out that in each case no adjustment has yet been made to account for the marked early-season vulnerability of young birds to the gun. In two of the formulas a second limitation may appear in occasional years when some extraordinary changes occur in the monthly variation of waterfowl mortality. (These apparently took place in both 1939 and 1946 in the Mississippi Valley when the percentage of adult mallards taken in October significantly exceeded that taken in November.)

Recovery Rates and Mortality Rates

Are these fluctuations in seasonal recovery rates, described above, actually correlated with annual mortality rates? To answer this question, mortality curves available for this period were compiled from birds banded in Manitoba, Saskatchewan, and the various states bordering the Mississippi River. Data obtained by the Illinois Natural History Survey were omitted, as this sample was being analyzed by Bellrose and Chase (1950). The hunters' reports involve only birds shot as adults and only those banded before September 1 of the year in which they were shot. While I have termed these birds "Mississippi Valley" mallards, one must remember that this term is an arbitrary one.

Computations of mortality rate were carried out for these adult birds on a time-specific basis. The limitations of this analytical method have been described in Chapter III, and the results given in figure 15 are therefore termed an index rather than a series of mortality rates. A fair degree of correlation with adult-recovery rate occurs in five out of the six years studied. In view of both the unreliability of time specific calculations and the small samples from which the recovery rates were taken, the correlation seems to me to be surprisingly close.

The accuracy of a Canadian first-season recovery rate as an index of hunting mortality in mallards is not readily susceptible of proof. Whatever its reliability, it is obvious that this rate can at best only concern the regional populations from which the birds were trapped and banded. It does not follow that mallards from Alaska, Yukon, Mackenzie, and British Columbia have recovery rates of a similar character. I do think we can conclude that, given sufficiently large samples and adequately randomized banding operations, seasonal recovery rates will fluctuate directly with the mortality rates in a waterfowl population.

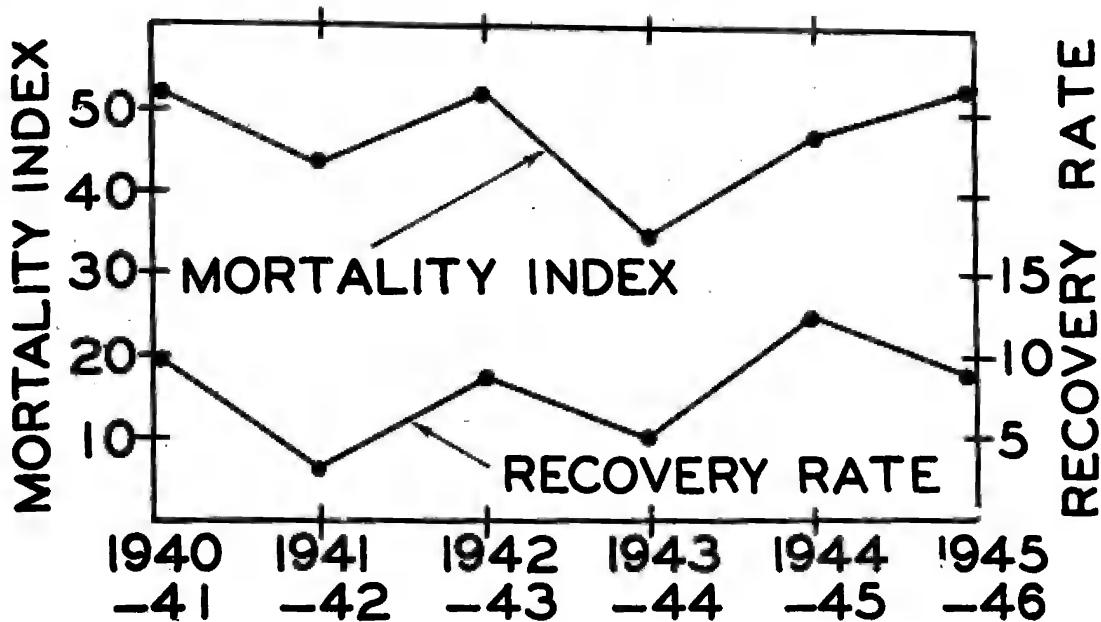


Figure 15.--Adult Mortality Index for Mississippi Valley
Mallards Compared to Adult Recovery Rates
for Birds Banded in Canada and Northeastern
Illinois

The exact statistical relationship between these two kinds of rates appears to require some detailed studies that could not be pursued within the time limits of my own project. If annual mortality rates can be estimated within reasonable limits by analyses of seasonal recovery rates, waterfowl managers have a life-table short cut of considerable importance in their evaluation of hunting regulations. Some crude data on the subject were available near the end of my study. These are given in a subsequent chapter.

Relative Geographic Abundance

Under certain conditions, the mortality data obtained from bird banding may be converted into an index of the relative abundance of two geographic populations of a migratory species. One might, for instance, attempt to determine that the breeding mallard population of Manitoba is x times as large as the breeding mallard population of Saskatchewan and y times as large as that of Alberta. A similar comparison might involve wintering populations in nearby regions. The conditions required for the calculation appear at this time to be as follows:

- (1) The two geographic populations to be compared must reside at one time of the year in nearby regions, such as Alberta and Saskatchewan; or in Texas and Louisiana.
- (2) During this period of residence, samples of the two populations need to be banded in sufficient size and apparently in a random manner.
- (3) After the birds have migrated, samples of the two populations must again be banded in some third region in sufficient numbers and apparently in a random manner. I term this third region the area of reference.
- (4) The species studied must, of course, possess a satisfactory recovery rate for each banding operation in order to provide enough recoveries for analysis.

In my work on the North American banding files, I encountered no banding operations that met these conditions when rigidly applied. Some of the mallard work may, however, serve as an illustration of how such a geographic index can be computed and perhaps emphasize its use in a carefully planned international system of bird-banding stations.

We can begin by comparing the breeding mallard populations of Manitoba and Saskatchewan. (Manitoba contains 246,512 square miles, Saskatchewan 251,700 square miles.) Adult mallards were banded from May or June through August 31 in the southern parts of these two prairie provinces; they roughly totaled 1500 for Manitoba and about 8000 for Saskatchewan, and at the present time cannot be safely regarded as randomized samples of the breeding populations of these two areas. The Manitoba sample is weak because the 1936-46 recoveries

in the legal hunting season number only 194; the 499 parallel Saskatchewan recoveries may be biased because so many of them represent birds banded at or near Yorkton.

In another paper (Hickey 1951) I have shown that, of 194 Manitoba-banded birds which were later reported, 15 per cent (actually 14.9 per cent) came from Arkansas and Louisiana, and that 17.6 per cent of 499 Saskatchewan recoveries were likewise reported from the same region. Now if the mallard populations breeding in these two Canadian provinces were exactly equal in numbers, and these two banding samples were perfectly randomized and free of sampling errors, it would follow that the ratio of Manitoba to Saskatchewan birds in Arkansas-Louisiana is as 14.9 is to 17.6. If the Manitoba population was twice that of the Saskatchewan one, the ratio would be as 29.8 is to 17.6. The actual ratio can be determined if randomized samples of the Arkansas-Louisiana population are banded and the number of breeding-season recoveries are tabulated for the two prairie provinces. From Hochbaum's (1944) work in Manitoba, I infer that the breeding season may be taken as the months of May, June, and July; the exact period when no significant number of transients are present deserves further study. No thoroughly randomized banding operations have been carried out in Arkansas-Louisiana, but the work of McIlhenny at Avery Island, Gordon at the Rainey Sanctuary, and Van Huizen at the White River Refuge may be used to continue the illustration. Of the mallards banded in Arkansas-Louisiana, 14 have been later reported in the "breeding season" in Manitoba and 17 in Saskatchewan. We therefore have an equation

$$\frac{14}{17} = \frac{0.149 M}{0.176 S}$$

with M and S the two unknowns. Here 0.97M = 1.0S. The result, that the mallard population of Saskatchewan is equal to 97 per cent of the mallard population of Manitoba must, of course, be subject to sampling variations and to potential biases already mentioned.

The pertinent details of a series of similar tests are given in table 56. Data furnished by the individual reference areas are often so few that the different results may well be the product of small-sample variations. I have no other satisfactory explanation for the divergent values given when Oklahoma is used as a reference area. G. A. Swanson has pointed out to me that the validity of these comparisons lies in the implication that the two migratory populations are banded in a reference area in which the migrants have become thoroughly mixed together. It would be improper in such analyses to consider North Dakota as a reference area in the comparison of birds breeding in two nearby areas like Saskatchewan and Manitoba.

The data and calculations given in table 56 illustrate a technique that could not be further explored in the present study. The birds banded in Canada (at least during midsummer) cannot be

Table 56.—Method of Comparing Relative Size of Two Migratory Bird Populations

I. Manitoba and Saskatchewan Populations of Mallards

Col (1) and (2) represent breeding-season recoveries (i.e., May to July inclusive) of birds banded in Illinois and the 4 other reference areas. Columns (3) and (4) are taken directly from a sample of 194 adult mallards banded in Manitoba; columns (5) and (6) show part of a sample of 499 adults similarly banded in Saskatchewan. The Missouri birds were banded in the 1920's; the Kansas birds mostly in the 1930's; all the others represent the period 1939-46.

Column Area of Reference	(1)	(2)	(1) (2)	(3)	(4)	(5)	(6)	(4) (6)	(1) (2)	(1) ÷ (4) (6)
	Reference Birds Recovered in		$\frac{M}{S}$	Recovered in Reference Areas				$\frac{1}{M}$	Manitoba Population Equals	
	Man.	Sask.		Man.		Sask.		$\frac{1}{S}$		
Missouri	9	7	1.3	11	5.7	20	4.0	1.4	0.9	Sask.
Ark.-La.	14	17	0.8	29	14.9	88	17.6	0.8	1.0	"
Kansas	5	20	0.3	2	1.0	17	3.4	0.3	1.0	"
Oklahoma	10	12	0.8	3	1.5	17	3.4	0.4	2.0	"
Subtotal	38	56	0.7	45	23.1	112	28.4	0.8	0.9	"
Illinois	73	43	1.7	19	9.8	30	6.0	1.6	1.1	"
Total	111	99	1.12	64	33.0	172	34.4	0.96	1.17	"

II. Alberta and Saskatchewan Populations of Mallards

The Alberta-banded birds (columns 3 and 4) are taken from a sample of 340 recoveries. The Saskatchewan-banded birds are part of a sample of 499.

Column Area of Reference	(1)	(2)	(1) (2)	(3)	(4)	(5)	(6)	(4) (6)	(1) (2)	(1) ÷ (4) (6)
	Reference Birds Recovered in		$\frac{A}{S}$	Recovered in Reference Areas				$\frac{A}{S}$	Alberta Population Equals	
	Alta.	Sask.		Alta.		Sask.		$\frac{1}{S}$		
Kansas	22	20	1.1	10	2.9	17	3.4	0.9	1.2	Sask.
Oklahoma	8	12	0.7	3	0.9	17	3.4	0.3	2.3	"
Illinois	19	43	0.4	6	1.8	30	6.0	0.3	1.3	"
Missouri	4	9	0.4	6	1.8	20	4.0	0.4	1.0	"
Ark.-La.	7	17	0.4	18	5.3	88	17.6	0.3	1.3	"
Total	60	101	0.60	43	12.7	172	34.4	0.37	1.62	"

reliably taken as breeding in the province in which they were banded. A. S. Hawkins and L. K. Sowls point out to me that the magnitude of mallard flights to molting lakes still requires much study. In this species at least, the breeding season cannot reliably be assumed to extend through July and August.

With these limitations in mind one may, however, conclude that on some occasions this technique will enable us to compare the relative size of migratory bird populations from mortality data alone. Given banding operations of sufficient magnitude, the right time, and the right geographic location, this formula should be useful:

$$A = \frac{B_c C_a}{A_c C_b}$$

where A and B are two regional populations to be compared for relative size

A_c = the percentage of birds banded in region A and recovered in a reference area C

B_c = the percentage of birds banded in region B and recovered in reference area C

C_a = the number of birds banded in C and recovered in area A

C_b = the number of birds banded in C and recovered in area B

Summary

The percentage of a banded sample shot during the first hunting season to which the birds were exposed is termed the first-season recovery rate (or the seasonal recovery rate). While this rate appears to be a good index of hunting pressure, it does vary from one banding station to another, the fluctuations being rather well synchronized from one year to the next. The juvenile first-season recovery rate may in some years be less than the adult one. Under such circumstances the difference can be used to furnish a minimal estimate of the amount of nonhunting mortality affecting the juvenile population before the start of the hunting season. Seasonal recovery rates for adult mallards appear to be correlated with the overall annual mortality rates. Their use as an easily computed mortality index offers considerable promise in wildlife management.

Under special conditions rarely encountered at the present time, the mortality data on banded birds can be used to calculate the relative abundance of two geographic populations of a given species. The conditions necessary for this analysis are described and a formula given to obtain the results.

Chapter XIII.--Variations in Mallard Mortality Rates

In Chapter VI, it was shown that 1230 adult mallards banded in the Mississippi Valley from 1922 to 1926 had a mean annual mortality rate of 46.5 per cent per year, while 1762 adult males banded on the Pacific coast from 1926 to 1935 had a mean average of 48.5. That this conformity is the result of averaging a wide variety of conditions can be seen in table 57, which brings out a significant difference between rates calculated for Pacific coast adults banded in 1926-30 and those banded in the next 5-year period. This convincing difference could mean that important differences in annual mortality rates occurred from one year to another, or that the heterogeneous collection of reports from different places on the Pacific seaboard contained regional differences that showed up in this fashion.

Variations Between the Sexes

Variation in mortality rates between the sexes was explored only at the start of the study. Time-specific estimates on birds banded in Oklahoma by H. S. Davis and R. H. Jordan permitted means to be calculated for the first 3 age intervals subsequent to banding. These are included in table 58 along with four other dynamic life-table computations derived from materials in the U. S. banding files and a fifth set recalculated from the literature.

It would appear from the few samples in this table that rather striking mortality-rate differences exist either geographically or chronologically for this species, and that two patterns involving different mortality rates for the two sexes are possible. Bellrose and Chase (1950) rightly ascribe the higher mortality rate in their sample to the probable vulnerability of females to predators during the nesting season. One naturally wonders if the higher mortality rates for males in the Pacific Flyway represent a greater selectivity of hunters shooting males in preference to females. This problem may be studied in table 59 which I compiled at the suggestion of A. S. Hawkins.

The differences in first-season recovery rates reported here (1.4 and 1.6 per cent) closely follow those evident in Bellrose and Chase's (1950) study of mallards banded at Lake Chautauqua Illinois: 6.3 per cent for 22,284 males and 5.0 per cent for 8628 females. These differences also increase in a similar manner as more years are added to the recovery periods. There is thus no evidence presented here that demonstrates any difference in hunter selectivity on the west coast and in the Mississippi Valley. We are left with the implication that nesting conditions encountered by the Pacific Coast birds reviewed here possibly differed from those postulated for the Illinois-banded birds studied by Bellrose and Chase (1950).

Table 57.—Hunters' Reports of Pacific Coast Adult Male Mallards

Birds known to be adult before start of hunting season. Most of these birds were unaged at time of banding. For birds banded in 1926, the hunters' reports begin as of the fall of 1927.

Cohort	Age Interval When Reported Shot											Annual Mort. Rate at Age Interval To- tal x+1 to x+2	
	x+1	x+2	x+3	x+4	x+5	x+6	x+7	x+8	x+9	x+10	x+11		
	x+2	x+3	x+4	x+5	x+6	x+7	x+8	x+9	x+10	x+11	x+12		
1926	29	9	6	-	1	1	1	-	-	-	-	47	-
1927	162	48	28	8	-	1	2	-	2	1	-	252	64%
1928	231	82	12	11	4	3	1	-	1	-	-	345	67%
1929	69	14	8	13	3	2	-	-	-	-	-	109	63%
1930	38	11	5	9	1	1	-	2	-	-	-	67	-
Subtotal	529	164	59	41	9	8	4	2	3	1	-	820	-
1931	29	19	8	1	-	2	-	-	-	-	-	59	-
1932	98	42	17	1	2	2	2	-	-	1	-	165	59%
1933	109	35	17	10	7	2	3	3	-	-	-	186	59%
1934	80	24	23	19	11	15	3	2	2	1	1	181	44%
1935	104	92	46	38	37	13	5	6	2	4	2 ^{1/}	349	30%
Subtotal	420	212	111	69	57	34	13	11	4	6	3	940	-
Total	949	376	170	110	66	42	17	13	7	7	3	1760	-

Survival Series: Birds Alive at Start of Each Year												Mean Mort. Rate for All Ages
1926-30	820	291	127	68	27	18	10	6	4	1	-	1372
1931-35	940	520	308	197	128	71	37	24	13	9	3	2250
Total	1760	811	435	265	155	89	47	30	17	10	3	3622

Mortality Rates (Per cent Per Annum)												Mean Mort. Rate for All Ages
1926-30	65	56	46	51	-	-	-	-	-	-	-	59.8
1931-35	45	41	36	35	45	-	-	-	-	-	-	41.8
1926-35	54	46	39	42	45	-	-	-	-	-	-	48.6

^{1/} estimated; this table was compiled before results for the fall of 1946 were available; the additional birds shot in subsequent years should not importantly affect the mortality rates calculated here.

Munro (1943) has reported that females rather consistently exceeded males in numbers banded by A. J. Butler in British Columbia, the sex ratio for 13,959 mallards being 45.7 per cent males against 54.3 per cent females. "Banding recoveries show that more females are shot than males; in a 12-year period the numbers recorded were 1299 females and 1277 males. Thus hunting probably is not a factor

Table 58.—Mean Mortality Rates for Male and Female Mallards

Where Banded	When Banded	Age at Start	Size of Sample		Mort. Rate % per year		Banders
			Male	Female	Male	Female	
Missouri	1923	Adult	169	98	46	47	L. V. Walton
Oklahoma	1938-41	Adult	592	279	46	47	Davis, Jordan
Illinois 1/	1939-44	Unaged	5606	1609	43.2	46.8	Ill. Nat. Hist. Survey
Montana	1928	Unaged	907	589	63.7	62.4	F. H. Rose
"	1928	Adult	343	204	60	57	F. H. Rose
British Col.	1931-39	Adult	614	560	68.5	65.5	A. J. Butler

1/ The mean mortality rates for Illinois were recalculated from original data compiled and adjusted by Bellrose and Chase (1950); their mortality rates for the two sexes, 41.78 and 46.68 per cent are arithmetic means covering rates for the first 5 age intervals; the ones shown in this table are geometric means calculated in the standard manner (see Chapter I).

Table 59.—Differential Recovery Rates for Unaged Male and Female Mallards

When Banded	Where Banded	Males			Females			Bander
		No. Banded	No. Shot	% Shot	No. Banded	No. Shot	% Shot	
1927	Mont. 1/	2127	416	19.6	1363	246	18.0	F. H. Rose
"	2/	2127	663	31.2	1363	380	27.9	F. H. Rose
1928	1/	4168	564	13.5	3176	385	12.1	F. H. Rose
"	2/	4168	898	21.5	3176	579	18.2	F. H. Rose
"	3/	4168	907	21.8	3176	589	18.5	F. H. Rose
1931-41 B.C.	4/	6308	1137	18.0	6886	1091	15.8	A. J. Butler
1936-44 S.D.	4/	6762	1257	18.6	4048	532	13.1	Sand Lake Ref.
Total 5/		19,365	3964	20.5	15,473	2592	16.8	

1/ Shot same season as banded.

2/ Shot in 5-year period.

3/ Shot in 10-year period.

4/ The number shot should be increased by additional reports after this tabulation was made.

5/ Excluding lines 1, 3, and 4 which in effect are subtotals only.

in the sexual unbalance suggested by these figures" (Munro 1943, p. 243). I am unable to follow Munro's reasoning on this point. The even sex ratio among the bagged birds, when compared to the unbalanced ratios found in the banding traps, clearly indicates that more males than females were taken by hunters.

Regional Uniformity

Some preliminary explorations of the banding data for the Mississippi Valley involved comparisons of mallard mortality rates for specific years. An example given in table 60 shows how fairly close in agreement many of these sample mortality rates were. Figure 16 demonstrates how 5 out of the 6 mortality series in this table displayed a marked relative increase in hunting reports for the year 1944-45. For the birds cited in table 60 this in the number shot represents an increase in mortality "rate" of the order of 20 per cent over the previous year (that is, from 39 for 1943-44 to 47 per cent for 1944-45). Although the comparison involves incomplete mortality data (in that additional mortality reports could be expected subsequent to the time of compilation), the mortality "rates" calculated for a given cohort are equally biased and general conclusions remain reliable.

Mallard mortality rates were also compared for two banding operations carried out by the Fish and Wildlife Service on different refuges in the same state, North Dakota. In 1939 C. J. Henry and Merrill Hammond banded 918 mallards of all sexes and ages at the Lower Souris National Wildlife Refuge. The mean annual mortality rate for 233 of these subsequently reported was 56 per cent. In the same year S. H. Low banded 4000 mallards at the Des Lacs National Wildlife Refuge; for 741 of these reported the mean annual mortality rate was 54 per cent. These means include both juvenile and adult birds shot the same season they were banded. The seasonal recovery rates for the two bandings differed: 15.3 per cent for Lower Souris, and 10.1 per cent for Des Lacs. Mortality rates calculated for the year 1939-40 were 56 per cent for the former, 55 per cent for the latter.

As Lincoln (1939, p. 164) and Hawkins (1949) have shown, the mallards in the Mississippi Valley are not an easily defined population unit. I finally assembled hunters' reports of this species for birds banded in the 3 prairie provinces and in the states actually bordering on the Mississippi River. The hunting covered from 1939-40 to 1945-46 inclusive. In this aggregation, 405 Illinois adults banded up to August 31, 1939, had a mean annual mortality rate of 46 per cent, identical to that of 457 adults banded elsewhere in this region. For the year 1939-40, the Illinois sample gave an annual mortality rate of 46 per cent, the non-Illinois sample 48 per cent. These were dynamic life-table calculations with 3 birds estimated as the mortality in 1947-48 and 1 estimated for 1948-49.

On the basis of this evidence, it would seem that aggregations of banding data for a species like the mallard display a geographic uniformity within a region and that they should be useful in analyzing changing mortality rates for specific years.

Table 60.—Geographic and Annual Variations in Annual Mortality Rates for Adult Mallards

These dynamic life-table compilations are abridged because not all the mortality data were available at the time the tables were compiled. In a few cases the number of deaths was estimated (see note no. 3). The incomplete mortality data make the rates calculated for the 1940 and 1941 cohorts higher than that obtainable from complete data. Each year begins September 1. Hunters' reports turned in by banders were excluded.

When Banded	Type of Statistic	Where Banded	Life-table Data by Specific Years									Mean Mort. Rate for 1st 2nd all yr. yr. yrs.			
			'40 to '41		'41 to '42		'42 to '43		'43 to '44		'44 to '45		'45 to '46		Total
			'40	'41	'41	'42	'42	'43	'43	'44	'44	'45	'45	'46	'47
1940	Numbers reported	Canada 1/	65	24	11	5	5	2	2	2	114				
		Illinois	110	51	35	20	18	8	3	3	245				
		as Oklahoma	142	55	42	15	14	12	6	3	286				
		shot Mo., Ark., La.	174	76	47	28	11	7	4	4	347				
		SUBTOTAL	491	206	135	68	48	29	15	15	992				
1940	Numbers alive at start of each year	Canada 1/	114	49	25	14	9	4	2	217	57	—	53		
		Illinois	245	135	84	49	29	11	3	556	45	38	44		
		Oklahoma	286	144	89	47	32	18	6	622	50	38	46		
		Mo., Ark., La.	347	173	97	50	22	11	4	704	50	44	49		
		SUBTOTAL	992	501	295	160	92	44	15	2099	49	41	47		
1941	Numbers reported	Canada 1/	61	35	16	10	2	11	11	135					
		Illinois	67	43	13	13	6	6	6	148					
		as Oklahoma	181	101	50	43	33	16	3	424					
		shot Mo., Ark., La.	136	63	33	22	25	9	9	288					
		SUBTOTAL	445	242	112	88	66	42	42	995					
1941	Numbers alive at start of each year	Canada 1/	135	74	39	23	13	11	295	45	—	46			
		Illinois	148	81	38	25	12	6	310	45	—	48			
		Oklahoma	124	243	142	92	49	16	966	43	42	44			
		Mo., Ark., La.	286	152	89	56	34	9	628	47	41	46			
		SUBTOTAL	995	550	308	196	108	42	2199	44.7	44	45			
1940- 1941	No. reported No. alive start	TOTAL	651	377	180	136	95	57	1196	2/					
	shot each year	TOTAL	1496	845	468	288	152	57	3306	2/					
1940	Mortality rate per annum		49	41	46	42	-	-	-	47					47
1941	"	"	44.7	44	36	45	-	-	-	45					45
1940-1941	"	"	43.5	45	38	47	62	-	-	45					45

1/ Prairie provinces only; Alberta is included in this sample but was dropped from subsequent samples designed to represent the Mississippi Valley population of mallards.

2/ Excluding the data for the year 1940-41.

3/ Estimated at a time when the data were not available.

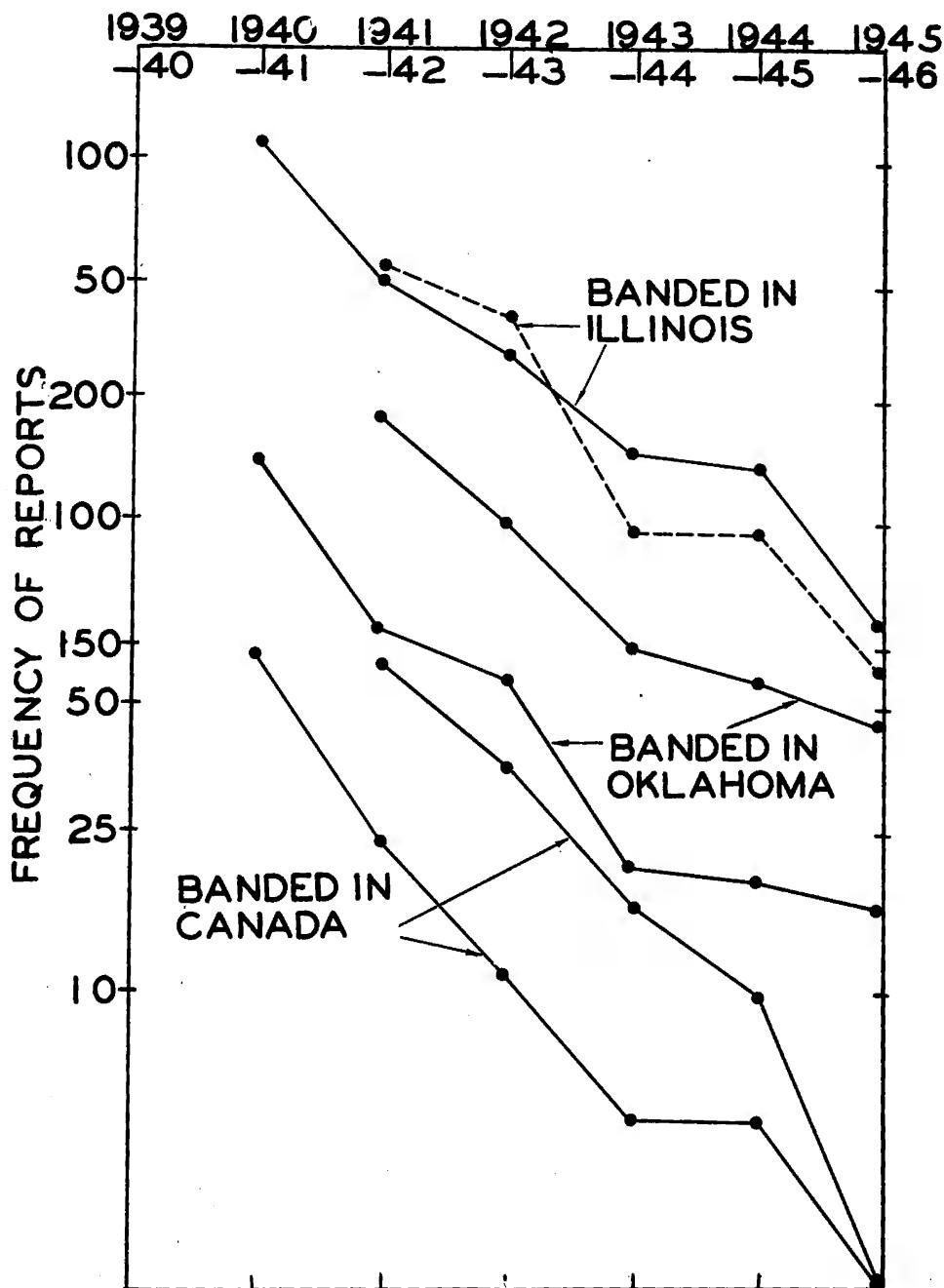


Figure 16.—Mallard Mortality Curves Based on Hunters' Reports of Birds Shot

Six of the eight mortality series in table 60 are shown here on semilogarithmic scales. Five of the curves show a marked increase in the number of deaths in the year 1944-45 over what normally would be expected. Each year begins September 1.

Limitations of the Data

In attempting to compute mortality rates for specific years (like the year 1939-40), one must realize that we are no longer studying the "theoretical" populations of Part II; all of these were banded over a period of years during which annually fluctuating mortality factors would appear as average environmental influences. The graphs showing recovery rates in Chapter 12 demonstrate that hunting mortality among mallards varies importantly from one year to another. When this information from hunters is either the only or the principal source of original data in a dynamic life table, how reliable are the annual mortality rates that are calculated for specific years?

This pertinent question is explored in table 61 by calculating what would happen to a cohort of 1000 hypothetical waterfowl when hunters kill anywhere from 15 to 35 per cent in different years.

Table 61.—Effects of Wild Hunting-pressure Fluctuations on Mortality Rate Calculations of a Single Hypothetical Cohort of Waterfowl

(These birds were assumed to have been banded in the summer of 1939; and a dynamic life-table analysis based on the shot sample is used below to calculate mortality rates for successive years each beginning September 1. Only a part of the original calculations are shown here.)

Years	1939-40	'40-'41	'41-'42	'42-'43	'43-'44	'44-'45
Alive at Start	1000	600	282	180	108	52
Per Cent Shot	20	35	15	20	35	25
No. Shot	200	210	42	36	38	13
Nonhunting Deaths (25%)	200	98	60	36	18	10
Total Deaths	400	308	102	72	55	23
Annual Mortality Rates (%)						
Actual	40	51	36	40	51	44
Life Table	36	59	31	33	54	42

Under the rigorous conditions thus laid down, it is clear that life-table mortality rates for specific years are of extremely limited reliability. For the most part, they do seem to reflect actual changes upward or downward, but these changes may be importantly exaggerated. It is only when recovery rates are relatively constant or when a series of cohorts is grouped together in a life-table that we can expect approximations of mortality rates actually occurring in wild populations.

General Trend: 1929 to 1938

It is evident in table 57 at the start of this chapter that the annual mortality rate of 64 per cent for age interval $x + 1$ to $x + 2$

in the 1926-30 bandings is a mean of conditions occurring from September 1, 1927 to August 31, 1932. The successive mortality rates of 64, 56, and 46 per cent for this cohort thus represent points on a 5-year moving average. The birds banded in the cohort from 1931 to 1935 represent similar average points for later years (1932-37, etc.). They are, in fact, a 5-year moving average that suggests a definite trend. The possibility that this might be associated with trends in bag limits or length of season is examined in figure 17. It is clear that we have here strong presumptive evidence for a correlation between mortality rates and hunting pressure throughout this period. While the separate effects of season or bag limit require a more detailed breakdown of the data, the increase in season and mortality rates at the right-hand end of the curves deserves notice. It is perfectly possible that these adult mallards might have become less vulnerable to gunning as they grew older, and that the change in mortality rates was in part due to this increase in experience and in part to hunting. This possibility will be explored in other samples.

Mortality Rates on the Pacific Coast

British Columbia and Oregon Birds.—This exploration of changing mortality rates was continued in a study of 1384 adult male mallards banded on the Pacific coast, chiefly by A. J. Butler in British Columbia and by George M. Benson and his colleagues in the Fish and Wildlife Service at the Malheur National Wildlife Refuge near Voltage, Ore. The raw mortality data are given in table 62, where they are converted into survival data, and mortality "rates" are calculated for all birds available. Thus for the year 1928-29, when 162 were reported shot out of a cohort of 252 banded in 1927, 9 birds were similarly reported out of a cohort banded in 1926 out of which 18 were known to be alive. We can say, then, that 171 were shot (162 - 9) out of 270 alive at the start (252 - 18). This technique of adding different cohorts to obtain a mortality rate for a given year I call the method of cumulative cohorts. It has the merit of using all the banding data available and increasing the size of samples for study. It has a potential defect in that it cannot always be defended as a random sample of the adult population, since in some years the proportion of rather old adults in the sample may depend on banding work in the past and so vary considerably. If increasing age and experience make for a higher survival rate in mallards, a long series of cumulative cohorts such as this one would tend to show progressively lower mortality rates. It should, however, at least betray marked increases in mortality rates when these occur in specific years. The rates based on cumulative cohorts (given at the bottom of table 62) did not differ by more than 3 percentage points from those calculated for single cohorts (shown in the last column on the right of this table).

The explanation for the changes in mortality rates for these Pacific coast mallards is at least partly evident in figure 18. The first sharp drop in rates occurred when a presidential proclamation cut the United States hunting season from 107 days to 30 days

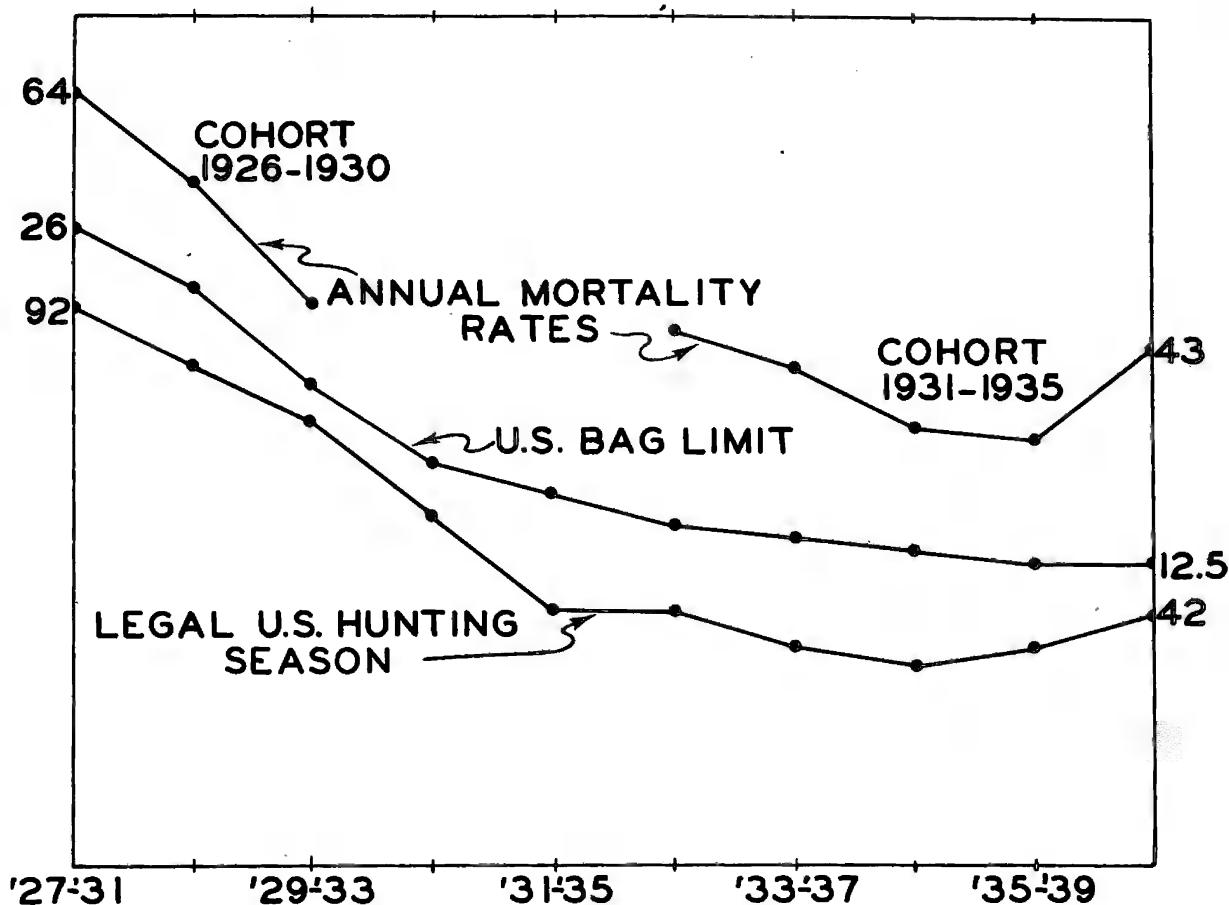


Figure 17.—Relation of Annual Mortality Rates to Hunting Pressure. Five-year moving averages of adult male mallard mortality rates for birds banded on the Pacific coast (table 57) are here compared with similar averages for the U. S. bag limit on waterfowl and the length (in days) of the legal U. S. hunting season in any given zone.

Table 62.—Variations in Adult Mallard Mortality Rates in 1928-35, Based on Hunters' Reports of Males Banded on the Pacific Coast

These birds were banded mostly by A. J. Butler in British Columbia and by G. M. Benson and his colleagues at the Malheur National Wildlife Refuge in Oregon. The last column on the right represents the annual mortality rate for first year indicated, based on a single cohort only (thus for birds banded in 1927, $162 \div 252$ equals 64 per cent for the year starting Sept. 1, 1928). Mortality rates at bottom of table are based on all banded cohorts available (thus 171 in the Total Shot column $\div 270$ in the Total Alive column equals 63 per cent for the year starting Sept. 1, 1928).

When Banded	Mortality and Survival Data Classified by Specific Years (IX/1-VIII/31)														Total q_{x+1}					
	'28	'29	'30	'31	'32	'33	'34	'35	'36	'37	'38	'39	'40	'41	'42	'43	'44	'45		
<u>Numbers Reported Shot</u>																				
'26	9	6	0	1	1	1												18		
'27	162	48	28	8	0	1	2	0	2	1								252	64%	
'28		231	82	12	11	4	3	1	0	1								345	67%	
'29			69	14	8	13	3	2										109	64%	
'30				38	11	5	9	1	1	0	2							67		
'31					29	19	8	1	0	2								59		
'32						98	42	17	1	2	2	2	2	0	0	1		167	59%	
'33							109	35	17	10	7	2	3	3				186	59%	
'34								80	24	23	19	11	15	3	2	2	1	1	181	64%
Total Shot	171	285	179	73	60	141	176	137	45	39	30	15	20	6	2	3	1	1	1384	
<u>Alive at Start of Hunting Season (September 1)</u>																				
'26	18	9	3	3	2	1												36		
'27	252	90	42	14	6	6	5	3	3	1								422		
'28		345	114	32	20	9	5	2	1	1								529		
'29			109	40	26	18	5	2										200		
'30				67	29	18	13	4	3	2	2							138		
'31					59	30	11	3	2	2								107		
'32						167	69	27	10	9	7	5	3	1	1	1		300		
'33							186	77	42	25	15	8	6	3				362		
'34								181	101	77	54	35	24	9	6	4	2	1	494	
Total Alive	270	444	268	156	142	249	294	299	162	117	78	48	33	13	7	5	2	1	2588	
<u>Mortality Rates (per cent per annum, September 1 to August 31)</u>																				
	63	64	67	47	42	57	60	46	-	-	-	-	-	-	-	-	-	53.5		

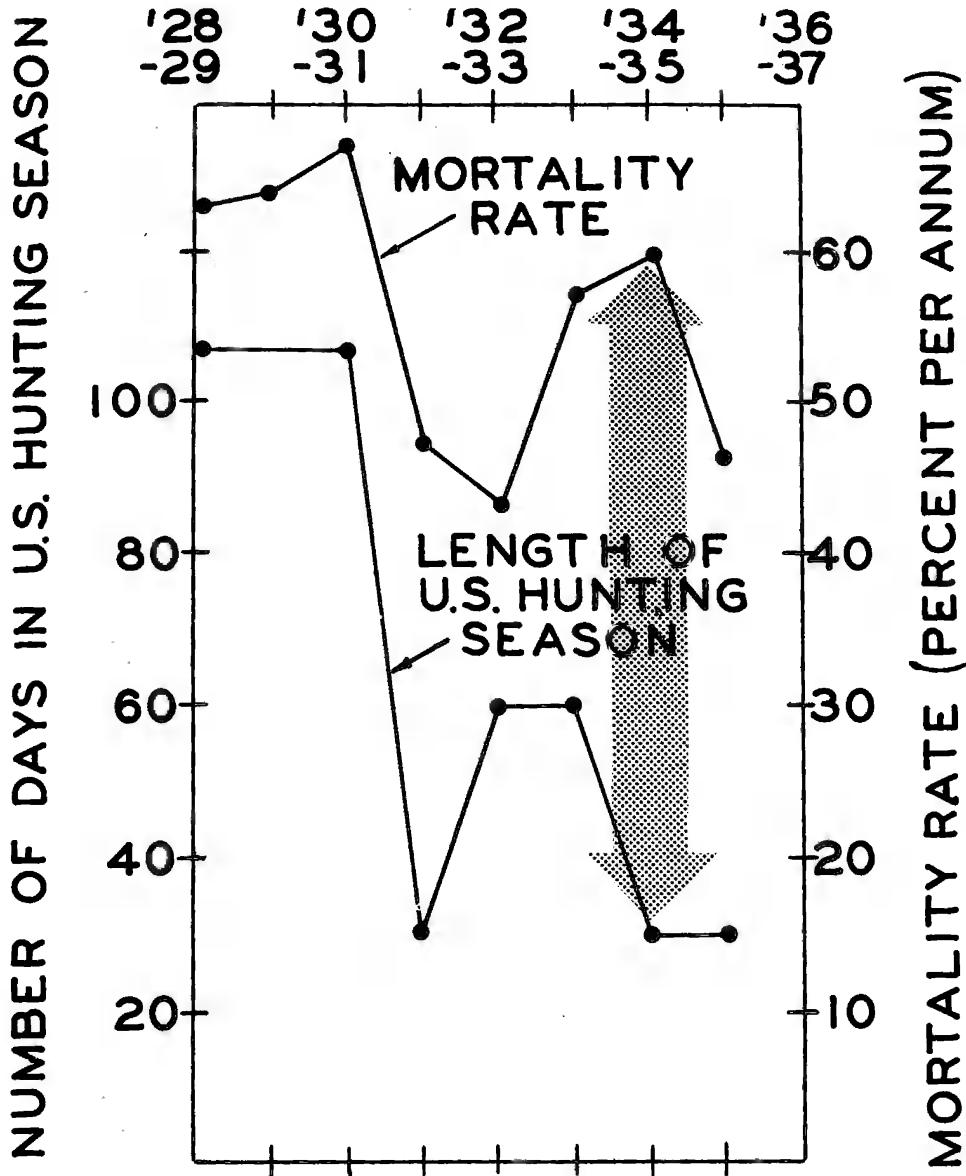


Figure 18.--Relation of Annual Mortality Rates (Adult Male Mallards Banded on the Pacific Coast) and Length of Hunting Season in the United States.
 Notice the lethal character of the staggered 30-day season in 1934-35. Each year begins September 1.

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in 1931. The data for this and the following year represent the smallest samples in the series here considered (156 and 142 respectively), and the precise effect of this drastic change in regulations must await study of a larger sample. The next important drop in mortality rate occurred when a staggered 30-day season was changed to a consecutive 30-day season. It would appear that the staggered 30-day season of 1934 was as lethal to these waterfowl as the 60-day season in 1933.

Western Montana birds.—As a check on the high mortality rates calculated from the British Columbia and Oregon bandings, an analysis was made of male mallards banded in the years 1926-29 by F. H. Rose in western Montana. This banding station has been included by Lincoln (1939, pp. 174-182) in his Pacific flyway. The mortality-rate comparison here contemplated should represent a new and rather critical test of the flyway as a population concept. Seven hundred and sixteen adult males banded in some year previous to the one in which they were shot had mortality rates of 63, 64, and 69 per cent for the years 1928, 1929, and 1930 respectively. Mortality data for 1655 males, which included juveniles and birds shot the same season as banded, yielded mortality rates of 62 per cent in 1927, 61 per cent in 1928, 60 per cent in 1929, and 69 per cent in 1930. My time did not permit a further expansion of these samples to include females; but as table 59 demonstrated earlier in this chapter, this is not a serious omission. The mean mortality rate for all males examined (62 per cent) agreed well with the 60 per cent calculated in table 57 for Pacific coast males. The Pacific flyway as a population concept appears to have withstood this test well. An even more important test involves the comparison of mortality rates between flyway populations.

Mortality Rates in the Mississippi Valley

Illinois and Missouri birds in the 1920's.—Adult mallard samples for both sexes were analyzed for birds banded by F. C. Lincoln in Illinois and John Broeker and L. V. Walton in Missouri from 1922 to 1926 inclusive. If band loss was frequently occurring in that early period, the calculated mortality rates should exceed those derived from more recent bandings. No such loss was evident. The rates computed for both sexes (table 63) were consistently lower than those for the males on the Pacific coast. The differences may or may not be attributed to my preoccupation with male birds in the more western samples. As a check on the fluctuations, I compared these Mississippi Valley mallard mortality rates with some first-season recovery rates reported by Lincoln (1930) for all species of waterfowl on the continent (figure 19). The agreement was sufficiently close to dispell any possibility that the rates are grossly inaccurate. I believe we must conclude that important fluctuations in the annual mortality rates of these banded adult birds took place during this period when hunting regulations were relatively stabilized and some other environmental factor was operating on these samples of the population. It seems to me

Table 63.—Variations in Mallard Mortality Rates Based on Hunters' Reports of Adults Banded in the Mississippi Valley During the 1920's

These birds were banded by F. C. Lincoln in Illinois and John Broeker and L. V. Walton in Missouri. As in table 62 the last column on the right is the annual mortality rate for first year indicated, based on single cohort only; mortality rates at bottom of table are based on all banded cohorts available. Durability of bands is unknown.

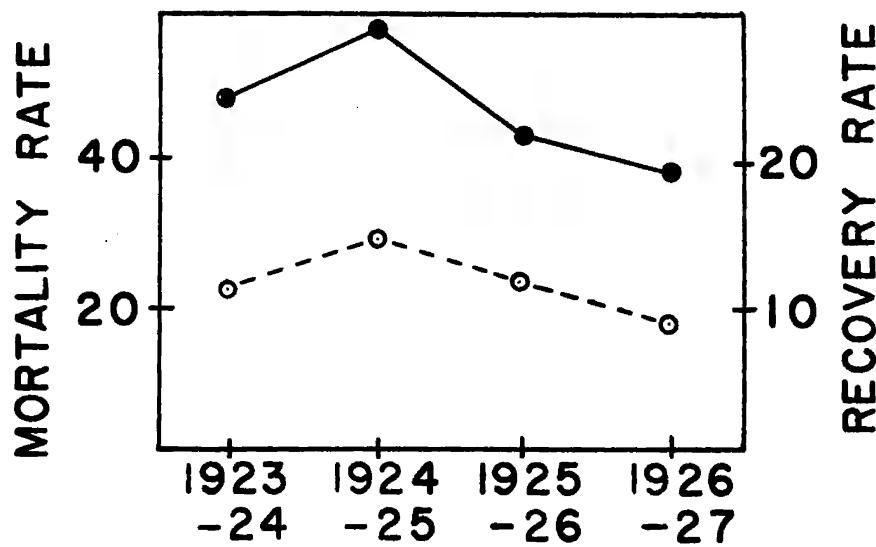


Figure 19.—First-season Recovery Rate (Broken Line) for All Waterfowl Banded in North America Compared to Adult Mallard Mortality Rates (Per Cent Per Annum) for Birds Banded in Illinois and Missouri (Solid Line).
 Each year starts September 1.

highly unlikely that the difference in mortality rates between the Pacific coast and Mississippi Valley birds is solely the result of sexual differences in the samples. The evidence points to different rates for the Pacific and Mississippi Flyway mallard samples examined, but absolute proof on this point was not gathered in the present study.

Illinois birds in the 1930's.--An interesting comparison with the 1920's is afforded by the banding of mallards by C. J. Goetz in Fulton County, Illinois, from 1933 to 1939 inclusive (table 64). A high overall mortality rate for the year 1934-35, when a split season governed hunting, may be due in part to chance. No marked fluctuations in mortality rates are evident from 1935 to 1940 inclusive. The mean annual mortality rate for 835 birds reported shot up to mid-1947 was 44.7 per cent in contrast to 46.5 per cent for 1185 banded in Illinois and Missouri during the 1920's.

Fluctuations in mortality reports in the 1940's.--By combining hunters' reports of birds banded in Saskatchewan, Manitoba, Minnesota, Wisconsin, Missouri, Illinois, Arkansas, and Louisiana (table 65), a preliminary picture can be obtained of fluctuations in adult mallard mortality rates for years (beginning on September 1) from 1939 to 1946. During this study the events were so recent that dynamic lifetable compilations were impossible, but a time-specific analysis should at least indicate the approximate nature of changes taking place in the samples. The basic data assembled are given in table 65, where it is evident that the survival-index values obtained with cumulatively totaled cohorts (part B of the table) are slightly higher than those obtained with single cohorts (part A of the table). This is another manifestation of a phenomenon noticed earlier in this chapter: increasing age in adult mallards makes for a decreasing mortality rate.

In figure 20 it is further evident that the survival-index values are inversely correlated with first-season recovery rates for mallards banded in Canada and northeastern Illinois. This does not mean that the index is an accurate substitute for survival rate, but it gives some assurance that the two statistics are measuring the same phenomenon. The time-specific mortality rates in table 65 average 47-48 per cent per year, in contrast to 43-47 per cent for unaged birds banded by the Illinois Natural History Survey during this same period (see table 58).

On the whole, it seems to me that seasonal recovery rates emerge from this discussion as being more reliable and more sensitive indicators of the effect of hunting regulations than survival indices computed by the time-specific method. There can be no doubt that important fluctuations in adult mallard mortality rates exist from one year to another, that they are measurable, and that they often reflect differences in hunting.

Table 64.—Sample Mallard Mortality Rates in the Mississippi Valley, 1935-1940

Based on adult birds banded by C. J. Goetz in Fulton County, Illinois. Each year starts as of September 1. Calculations as in table 62.

When Banded	Mortality and Survival Data by Specific Years												Mort. Rate for 1st yr. in cohort	
	'34	'35	'36	'37	'38	'39	'40	'41	'42	'43	'44	'45	'46	
<u>Numbers Reported Shot</u>														
Mar. '33	7	1	4	3	3	1	-	-	-	-	1	-	-	20
Mar. '34	60	30	18	5	5	4	1	-	-	-	-	-	-	123
Mar. '35	17	3	4	1	-	1	-	-	-	-	-	-	-	26
Fall '35	69	34	22	13	5	3	3	1	1	-	-	-	-	151
Dec. '36		114	56	28	25	14	7	5	3	3	1	256	-	45
Mar. '38			12	7	6	1	1	1	-	-	-	-	-	28
Dec. '38				63	30	15	9	7	5	2	-	131	-	48
Dec. '39					42	16	20	9	6	6	1	100	-	42
Total Shot	67	48	94	160	99	116	110	49	40	23	16	11	2	835
<u>Alive at Start of Hunting Season (September 1)</u>														Mean Mort. Rate All Ages
Mar. '33	20	13	12	8	5	2	1	1	1	1	1	-	-	65
Mar. '34	123	63	33	15	10	5	1	-	-	-	-	-	-	250
Mar. '35	26	9	6	2	1	1	-	-	-	-	-	-	-	45
Fall '35	151	82	48	26	13	8	5	2	1	-	-	-	-	336
Dec. '36		256	142	86	58	33	19	12	7	4	1	618	-	41
Mar. '38		28	16	9	3	2	1	-	-	-	-	-	-	59
Dec. '38			131	68	38	23	14	7	2	-	-	283	-	46
Dec. '39				100	58	42	22	13	7	1	1	243	-	41
Total	143	102	205	367	235	267	251	141	92	52	29	13	2	1869
<u>Annual Mortality Rate All Cohorts</u>														44.7
	47	47	46	44	42	43	44	(35)	-	-	-	-	-	44.7

Table 65.—Hunters' Reports of Adult Mallards Banded in the Mississippi Valley,
1939-46

Saskatchewan, Manitoba, and 6 states bordering the Mississippi River (Minn., Wis., Mo., Ill., Ark., La.) represented the area in which these birds were banded. Each year starts as of September 1; birds banded during the hunting season and hunters' reports turned in by the bander were excluded.

Cohort	Years when Birds Were Reported Shot								Time-specific Survival Index for 1st Yr. in Series		
	1939	'40	'41	'42	'43	'44	'45	'46			
<u>Numbers Reported Shot</u>											
A	1939	384	187	102	57	29	26	12	7	804	49
	1940		316	136	89	50	29	16	7	643	43
	1941			252	137	70	49	37	25	570	54
	1942				105	37	22	14	9	187	(35)
	1943					178	111	66	36	391	62
	1944						360	169	70	599	47
	1945							268	126	394	47
<u>Total Mortality (Time-specific Survival Series)</u>											
B	1939-40	384	187								
	1939-41		503	238							
	1939-42			490	283						
	1939-43				388	186					
	1939-44					364	237				
	1939-45						597	314			
	1939-46							582	280		
<u>Index for 1st Yr. in Series</u>											
<u>Survival</u>											
<u>Mortality</u>											
49										51	
47										53	
58										42	
48										52	
65										35	
53										47	
48										52	

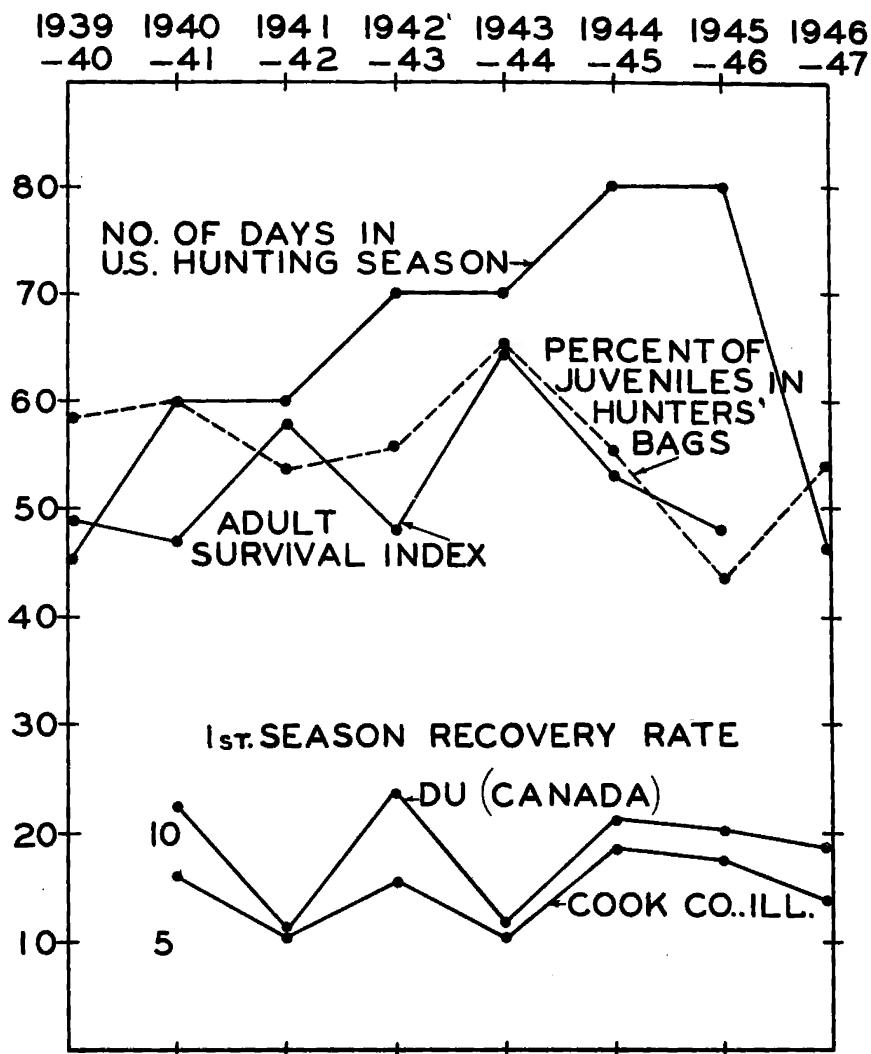


Figure 20.--Associations of Survival of Adult Mississippi Valley Mallards in the 1940's

Annual survival rates (starting as Sept. 1) are here approximated by a survival index (described in Chapter III). The percentage of juveniles among mallards shot by hunters was obtained in the Illinois River Valley by personnel of the Illinois State Natural History Survey (Hawkins, in litt.). First-season recovery rates are for unaged mallards (from figure 14). Interpretation: No general relation of adult survival rate and length of hunting season in the United States during this period is evident. Because the period began when the population was thought to be high, the lack of association between adult survival and annual production of young is to be expected during the years 1939-40 and 1940-41. The gradually increasing association of these two statistics could be explained as a chance phenomenon or as the result of a population decline in which the proportion of juveniles in the population became more and more important.

Summary

For 19,365 male mallards and 15,473 female mallards, banded from 1927 to 1944 in British Columbia, Montana, and South Dakota, recovery rates were 23.5 and 19.2 per cent respectively. The difference is believed to reflect the tendency of hunters to shoot males in preference to females, and closely follows that reported for Illinois-banded birds in the 1940's. A slightly higher mean mortality rate for males was found in two samples of British Columbia and Montana-banded birds. Mortality rates for Missouri- and Oklahoma-banded mallards tended to show females as having the higher rates, but the difference was not conclusive.

Analyses of banded samples of mallards disclosed no striking differences in mortality rates between adults banded at different localities in a given geographic region; in a number of cases the similarity was striking. An equally striking similarity was evident in five years for birds banded at widely separated places.

Mortality rates derived for specific years from life tables based upon a single source of data (like hunting) are quite unrealiable if this mortality factor is violently fluctuating from one year to another.

During the latter part of the 1920's, male mallards banded on the Pacific seaboard suffered annual mortality rates around 65 per cent. Males banded in western Montana had rates of the same magnitude. Samples of both sexes banded in the Mississippi Valley sustained much lower rates, their mean being 46.7 per cent. The evidence thus far assembled points to different mortality rates for different flyways during this period.

After 1930, adult male mallard mortality rates dropped about one-third on the Pacific seaboard, particularly in response to limitations on the length of hunting season in the United States. A split season of 30 days in 1934 seems to have been fully as lethal to these birds as the 60-day season that preceded it and contributed to an overall annual mortality rate that was about one-fourth or one-fifth higher than in the year that followed. The same phenomenon was evident for birds banded in the Mississippi Valley. From 1935 to 1940, mortality rates for Illinois-banded birds ran close to 44 per cent. Larger samples from numerous bandings in the Mississippi Valley yielded crude estimates of overall rates of 47 to 53 per cent during the 1940s when hunting regulations were being relaxed. Recent fluctuations in adult survival rates were noticed to be associated in two or three years with hunting regulations and in one year with a marked increase in the production of young.

Chapter XIV.--Dynamics of Mallard Populations

Effect of Hunting on Adult Mallard Mortality Rates

What percentage of the North American waterfowl population is annually harvested by hunting? Attempts to get this percentage directly have not yet been satisfactory. The total kill is also difficult to sample, and the amount of crippling losses is still unknown. Bellrose (1945) has published an interesting estimate that the total annual kill of the continental duck population is about 11 per cent. This statistic was based on (1) first-season recovery rates of waterfowl banded in Canada by Ducks Unlimited; (2) a correction factor allowing for 75 per cent of recovered bands being reported; and (3) an estimate that hunters retrieve only 75 per cent of the ducks they kill, 25 per cent being lost by "crippling." It must be obvious from the very considerable fluctuations in adult mallard mortality rates studied in relation to hunting in this chapter that Bellrose's estimate is probably too low. It is dangerous, of course, to generalize from the specific (in this case, adult mallards) to a continental population embracing all the waterfowl in North America.

Bellrose's commendable attempt can, however, be shown to have a real or potential weakness at each step of his calculations: (1) the recovery rates used seem to include birds banded during the hunting season; notice in table 55 (Chapter XII) the difference in mallard rates I use for Ducks Unlimited birds and those quoted there from Bellrose's (1944) paper; (2) the correction for unreported bands involves an unwarranted assumption pointed out in Chapter XII; (3) the 33 per cent correction factor for crippling loss (equivalent to 25 per cent of all the birds dying from hunting, although frequently mentioned by waterfowl biologists, nevertheless remains a guess.

More recently Bellrose and Chase (1950) have presented some interesting manipulations of band-recovery data that "indicate" hunting mortality annually affected 41 per cent of the 30,912 mallards banded at Lake Chautauqua, Illinois, from 1939 to 1944. This conclusion importantly rests upon an experiment in which a control series of 242 standard bands yielded a recovery rate of 8.7 per cent in contrast to 200 special reward bands that yielded a recovery rate of 25 per cent. The implication, that only 35 per cent of Canadian and U. S. hunters report the bands they obtain, would appear to be potentially affected by fairly large sampling errors, and I regard this Illinois result as a wholly preliminary one. When the final results of this reward-band experiment by the Fish and Wildlife Service and its cooperators are reported from other parts of the continent, the samples should be large enough to permit more confident estimates of the fraction of mallard populations bagged by hunters. Eleven per cent is clearly too low, and 41 per cent is quite possibly too high.

It seems to me that the annual kill of waterfowl can also be reliably ascertained if we ignore the actual extent of the two unknowns, unreported bands and crippling losses, and obtain in future studies of banding statistics the precise relation of seasonal recovery rates to overall annual mortality rates. A hypothetical case will illustrate the kind of results that can be expected from such an analysis.

In figure 21 I have plotted annual mortality rates for certain adult mallard populations (on the ordinate) against certain first-season recovery rates that were available to me at the end of this study. A regression line expressing the interrelationship of these two rates has been drawn on the graph from A to B. In no case did I have actual recovery rates taken from the same samples in which mortality rates were also available. These data are therefore crude ones, but they do bring out the nature of the statistics that other investigators can obtain with this technique and more precise facts. The line AB represents the total overall mortality rate per year. It has been drawn in here purely by visual inspection. This line means that a seasonal recovery rate of about 20 per cent would occur when the overall mortality rate was 70 per cent. Similarly with a first-season recovery rate of zero the overall mortality rate would be about 20 per cent per year. The slope of this line probably varies slightly when the data are segregated from different banding stations. Point A can be recognized as an upper limit of nonhunting mortality occurring in the population. If a line from point A is next extended parallel to the abscissa, this will intersect the ordinate on the right at D. Line AD can be said to represent that fraction of the population that is annually lost through nonhunting factors. It is likely that nonhunting mortality does not have the inflexibility implied in this diagram. It does, however, give us for the first time a working statistic in our exploration of population of this species.

A third step is to construct line AC because recovery rates up to 20 per cent are included in this diagram. C can be set as 20 percentage points above D. AC can now be regarded as a recovery rate-line over and above the fraction of the population lost from nonhunting causes. The area ACD therefore represents mortality that is normally reported to the Fish and Wildlife Service by the banding program.

The area ABC includes mortality involved in crippled and unretrieved birds and such dead banded birds as are retrieved but never reported to the government.

The area ABD represents the total fraction of the population dying because of hunting factors. It should be borne in mind that the mortality rates used to prepare this graph represent that percentage of the total population dying between September 1 and August 31. The various areas in this graph therefore represent fractions of the total population dying for the reasons here assigned.

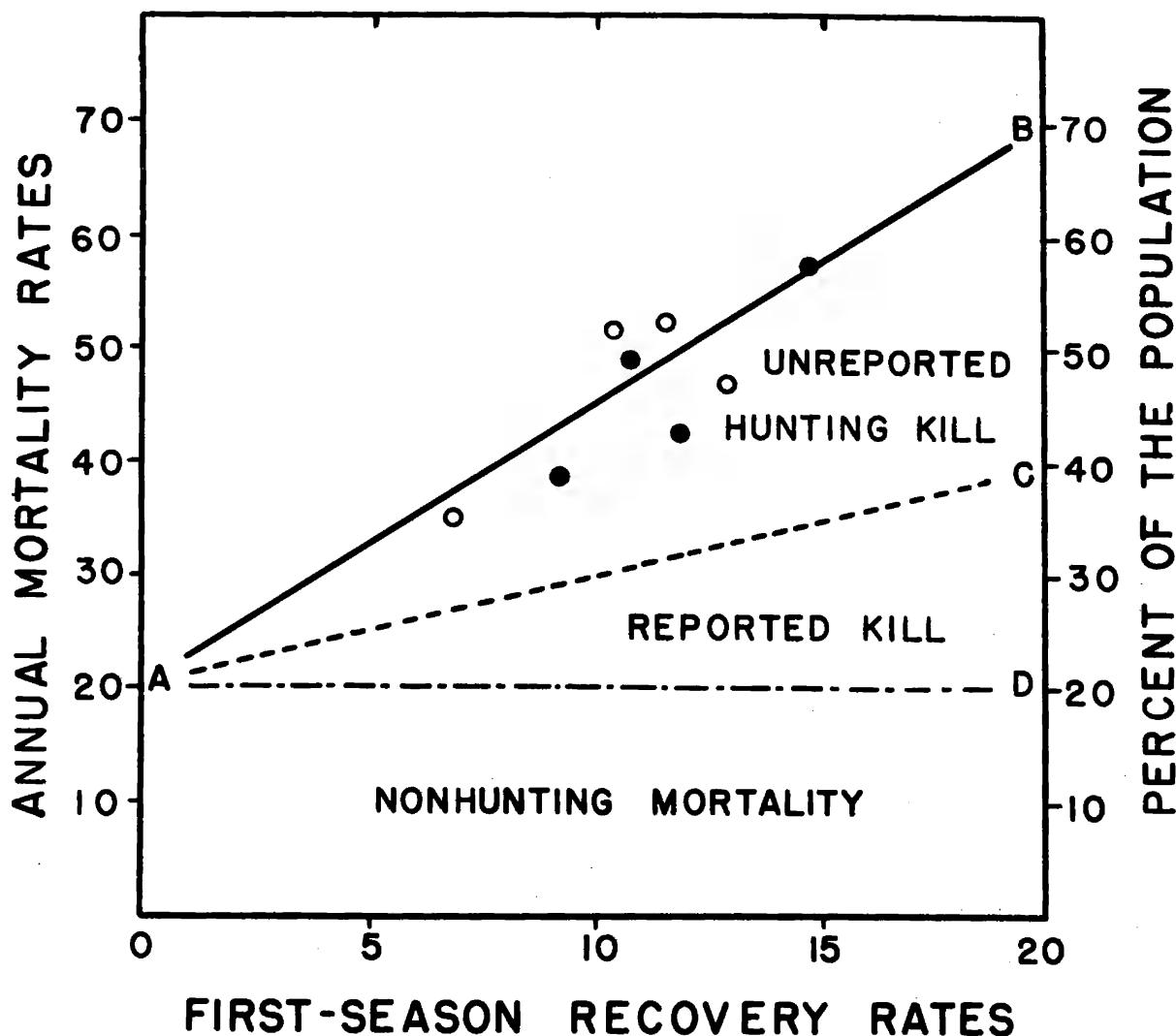


Figure 21.—Suggested Method for Determination of the Percentage of Waterfowl Killed by Hunters

Precise data on this problem were not gathered in the present study. Solid dots represent adult Mississippi Valley mortality rates for 1923-26 (table 63) for mallards plotted against first-season recovery rates for continental waterfowl obtained in this period and cited by Lincoln (1930); open circles represent estimated adult mallard mortality rates for 1940-46 (obtained by time-specific analyses in table 65) plotted against first-season recovery rates for unaged mallards banded in Canada before the start of each hunting season. The points A, B, C and D are explained in the text.

The refinement of this analysis represents a study which could not be incorporated into my own project. It should be obvious that so-called sampling limits or confidence limits can eventually be computed for line AB. Once these are established, a given first-season recovery rate could be determined each spring and a reasonable set of statistics derived for the past hunting season. Thus if figure 20 were based on precise data and not crude ones, a recovery rate of 12 per cent would indicate an annual mortality rate of about 50 per cent and a loss of about 30 per cent of the population due to hunting. Under such conditions and with precise data, the relationship of reported to unreported kill should be readily computable.

It is my feeling that the dynamics of adult mallard populations do, in fact, involve statistics with these relationships and that the ultimate determination of point A on the ordinates of graphs such as figure 20 can be readily determined.

Population Dynamics in the Mallard

Contemporary nesting statistics.--From J. B. Low's (1945) work, we have seen that in the redhead, clutches averaged 9.8 eggs, that 45 per cent of these produced young, and that juvenile losses to August 20 or September 1 averaged about 30 per cent. In the mallard, recorded mean clutch size is lower--about 7.8 (table 24) with 55-70 per cent of the nests hatching. The observed brood size for downy young is about 7.6 (table 26), and 20 per cent is the maximum mortality thus far reported from the time the young are downy to the point when they are able to fly (Stoudt 1946). A separate estimate, calculated in Chapter XII from recovery-rates in table 55, suggests a juvenile mortality rate of about 27 per cent from the time of banding to the start of hunting. Thus for these two species of waterfowl, the summer mortality of young birds appears to be roughly similar--about 25-35 per cent.

The immediate implication of this comparison is that redheads have larger clutches and lower nesting success in contrast to smaller clutches and higher nesting success in the mallard. The contrast is hardly a fair one. The redhead data come from an intensively studied area in Iowa, the mallard data from extensive studies scattered over a continent. Lyle K. Sowls (in litt.) sends me the following unpublished facts about mallard egg sets intensively studied at Delta, Manitoba: "Of 51 mallard nests known to have complete sets, the average was 9. Of 23 complete sets prior to June 15, the average was 10.0." Whitherby, Jourdain, Ticehurst and Tucker (1939) report that clutch size is "usually about 10 or 12, but may be any number from about 7 or 8 to 16." Bent's (1923) figures are substantially the same. There are thus good reasons to believe that a mean clutch size of 7.8 eggs for this species must refer importantly to renests (in which clutch size will average lower than first nests).

The initial size of mallard egg sets, the percentage of hens renesting, the percentage of success in each attempt are field statistics that are unavailable at the time of this writing. One can ask, "Would a mean clutch of 7.8 eggs suffice to balance a mallard population?" This can be studied by calculating what happens when only one nesting attempt is made by 100 pairs in a given breeding season (table 66).

Table 66.—Dynamics of a Hypothetical Mallard Population

(a) 100 pairs lay clutches averaging 7.8 (table 24)	780 eggs	-
(b) 55% of these (table 24) hatch as broods of 7.6 (table 26)		- 418 young
(c) about 30% of these (27% in Chapter 12) die by Sept 1. This leaves:	- - - 293	-
(d) about 32% of the remaining survive one more year (table 28):	- - -	94
(e) 100 pairs represent 200 birds at start of nesting	200	- - -
(f) 90% (this is a guess) survive to September 1	- - - 180	-
(g) 51.3% (this chapter) survive one more year	- - -	<u>94</u>
(h) Total		186

Readers who have followed the mallards accounts thus far set forth in this report will recognize that many of the statistics used in this tabulation are crude ones. We do have here, I think, all the pertinent productivity and mortality data available as of 1948. In the rough picture of population dynamics in this species emerging at this point, we see that the 186 survivors on the final September 1 (line h) are approximately the same in number as the 180 adults alive one year earlier (line f). The general statistics roughly approach that of a stable population. The present evidence thus points to a mean clutch of 7.8 as sufficient to balance mallard populations. Since it is apparent, as Sowls (in litt.) points out, that initial clutches of this species average much larger (10 or 11), it would seem that renesting is commonly resorted to in this species. Although its statistical dimensions still remain blurred, the picture sensibly agrees with that of a persistently early-nesting species which has ample time to renest annually (Hochbaum 1945).

It therefore seems best at this time to reject the idea that mallards have smaller clutches than redheads and that they overcome this handicap by achieving a higher percentage of nesting success. The two species appear to lay sets with about the same number of eggs. The mallard lays earlier, and it appears to do so for a good reason.

Fall and winter age ratios.—The accumulation of data on age ratios among waterfowl bagged by hunters almost took on the aspects of a major industry during the latter part of the 1940's. The data are extremely difficult to analyze, and I want to acknowledge at this time the vast amount of unpublished information that A. S. Hawkins, H. A. Hochbaum, and L. K. Sowls supplied to me on this subject.

There are at least two important reference points that life-table analyses can provide in the analysis of these phenomena. The first of these is some sort of average figure on the ratio of young to adults alive in the population as of September 1. The 1.6 young per adult implied in table 66 (293 in c, divided by 180 in f) must be regarded as a preliminary estimate only. This statistic owes its origin to table 28, where 163 wild-reared young birds were shown to be alive on September 1 as against 103 adults. A better estimate awaits the creation of a larger sample and a clearer picture of juvenile vulnerability to the gun.

A second reference point is the age ratio probably needed to keep mallard populations balanced; this can now be approximated as holding for birds alive at the end of the hunting season. The reasoning is quite simple. Over a period of 21 years, four large-scale banding operations are known to have involved a mean annual mortality rate of 48.7 per cent per year for adult mallards (table 67).

Table 67.—Adult Mallard Mortality Rates in the Aggregate

Where Banded	Period of Study	Number Alive at start	Number Dying	Mean Annual Mort. Rate (% Per Year)	Reference
Pacific Coast	1927-46	3622	1760	48.6	Table 57
Ill. and Mo.	1924-37	2547	1185	46.5	Table 63
Western Montana	1928-37	951	597	62.8	This Study
Illinois	1933-46	1869	835	44.7	Table 64
<u>Totals and Mean</u>		<u>8989</u>	<u>4377</u>	<u>48.7</u>	

Now if we can assume that this 20-year period contains about an even number of fluctuations in population level both up and down, we can say that this average mortality rate is our best presently available estimate of the average percentage of adults annually lost in this species. Under these conditions, stable populations will be maintained if by February 1 they average 51.3 per cent adult and 48.7 per cent young. Thus a mid-winter age ratio of 0.95 young per adult is our best estimate of what is required to balance mallard populations under "average" conditions.

These ratios refer to birds alive in the population. Their relation to age ratios among birds that are dead can be seen in table 68. Under whatever conditions we select, the ratio

of young to adults in hunters' bags will exceed that found in the population so long as this ratio among birds alive is a changing and shrinking one.

Table 68.—Some Potential Age Ratios for Mallards in Hunters' Bags

This table illustrates some age ratios to be expected in hunters' bags over an entire hunting season when a ratio of 1.6 young per one adult in the population on September 1 is reduced to 1 young per adult by February 1. A second assumption is made on column 2 for each line regarding the percentage of adults dying from hunting; from these the other figures follow.

<u>(1)</u> % of Age Class Shot	<u>(2)</u> Age Class Shot	<u>(1) ÷ (2)</u> Relative Vulnerability Over Entire Season	<u>(3)</u> Relative Nos. Shot From 160	<u>(4)</u> Nos. Shot From 100	<u>(3) ÷ (4)</u> Age Ratio in
					Hunters' Bags (Yg. per 1 Ad.)
46.9	15	3.1	75	15	5
50.0	20	2.5	80	20	4
53.1	25	2.1	85	25	3.4
56.2	30	1.9	90	30	3
59.3	35	1.7	95	35	2.7
62.5	40	1.6	100	40	2.5

This principle is well summed up in table 69. In this tabulation I have included an age ratio necessary to balance the mortality rates recalculated in table 58 for Illinois-banded reported on by Bellrose and Chase. Although their work covers a relatively short period, the result gives a fairly consistent picture. (I interpret their work as holding for late autumn since a critical correction factor used in their calculations is based on birds shot in the latter part of the hunting season.)

Two or three important variables govern age ratios in waterfowl and deserve mention. In the first place, differential migratory behavior can easily distort age ratios as indices of population structure; at A. S. Hawkins' request I reviewed the banding data on this point in 1947 but found the results to be inconclusive (not enough mallards had been banded as young at that time). The phenomenon is widely suspected but as yet little understood.

A second variable is the vulnerability of young birds to hunting (see column (1) + (2) in table 68). Is this a gradually or an erratically decreasing phenomenon during the autumn? I gather that it may well be erratic due to the great differences in the opening dates of hunting that occur between the various states and provinces.

Table 69.--Some Age Ratios in North American Mallards--
Real and Implied

Type of Birds	Living				Dead	
Source of Data	Life Table				Hunters' Bags	
Time Implied	Sept. 1	(Late Fall)	Feb.	Early Fall	Late Fall	
Period Studied	1925-46	1939-47	1940-47	1924-46	1939-41	1945-49
Where Secured	No. Am.	Ill.	Ill.	No. Am.	Man.	Ark.
Size of Sample	163	5606♂	2257	4377	1270	++
		1609♀				
Young Per Adult	1.6	.76-.88	0.91	0.95	2.2	1.45*
Per Cent Young	61	43-47#	47.6	48.7	69.5	59.2
Reference	Table 28	Bellrose and Chase (1950)		Table 67	Hochbaum (1944)	Hawkins (in litt.)

* arithmetic mean of ratios for 5 separate years

recalculated as per table 58

Using column (3) ÷ (4) in table 68 as a very rough sort of guide, we can now examine in table 69 the age ratio of 2.2 young per adult reported from Manitoba hunters' bags by Hochbaum (1944). This ratio would seem to suggest either less-than-average production in 1939-41 or differential migration by the young birds. The ratio of 1.45 young per adult found by Hawkins (table 69) in Arkansas would appear to demonstrate better-than-average production in 1945-49.

Annual adult mortality rates.--As I have pointed out in the discussion of table 61, no reliable method for measuring mortality rates for specific years emerged in this study. That these rates do vary widely from one year to another cannot be doubted. In table 70, I have gathered together some mortality "rates" based on a series of cohorts (birds banded in separate years). These approximations of what is occurring in mallard populations seem to suggest that at least during this period mortality in this species was by no means a local phenomenon. They are also a clear warning that comparative mortality rates for two species of waterfowl are most reliable when based upon birds banded during the same period.

Table 70.--Comparison of Adult Mortality "Rates" for Different Regions

Data from materials in Chapter XIII. Each year starts as of September 1.

Where banded	Mortality Rates Calculated for Specific Years							
	'28	'29	'30	'31	'32	'33	'34	'35
B. C. and Ore. (♂)	63	64	67	47	42	57	60	46
Montana (♂)	63	64	69	-	-	-	-	-
Illinois	-	-	-	-	-	-	47	47

Annual fluctuations in population levels.--The degree to which mallard populations will fluctuate is obviously a function not only of changes in annual mortality rates but also those yearly changes involving productivity. The interrelationship of these two variables is set forth in table 71. From unpublished data furnished by A. S. Hawkins of the U. S. Fish and Wildlife Service, I find that the annual productivity of mallard populations (as indicated by bag analyses in Arkansas) do vary within the magnitudes set forth in this table. One should notice then that with adult mortality rates of 40 per cent per year, population increases may be anywhere from 2 to 80 per cent; the difference between these two is 78 per cent. On the other hand, with a 65 per cent adult annual mortality rate, the variation in population levels covers 45 per cent (from -40 to +5). From this we may conclude that maximum fluctuations will tend to be more associated with differences in productivity than with variations in adult mortality. The recent research emphasis on productivity analyses of waterfowl is an important reaction to Hawkins' results along these lines.

Table 71.--Annual Changes in Level of a Population of Even Sex Ratio

This table illustrates the magnitude of population fluctuations to be expected in mallards. Thus when young number 0.7 per adult (i. e. 41 per cent of the population) at the end of the hunting season, the population will increase 2 per cent if the adult mortality rate is 40 per cent per year; it will decrease 6 per cent if this adult mortality rate is 45 per cent per year.

Annual		Number of Young Per Adult at End of Hunting Season													
Adult	Mort.	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
40	2	8	14	20	26	32	38	44	50	56	62	68	74	80	
45	-6	-1	4	10	16	21	26	32	38	43	48	54	60	65	
50	-15	-10	-5	0	5	10	15	20	25	30	35	40	45	50	
55	-24	-19	-14	-10	-6	-1	4	8	12	17	22	26	30	35	
60	-32	-28	-24	-20	-16	-12	-8	-4	0	4	8	12	16	20	
65	-40	-37	-34	-30	-26	-23	-20	-16	-12	-9	-6	-2	2	5	
<u>% Young</u>		<u>in Pop.</u>													
41	44	47	50	52	55	57	58	60	62	63	64	66	67		

Summary

A possible correlation was found between annually fluctuating mortality rates for adult mallards and variations in first-season recovery rates. A potential method of obtaining the percentage

of a banded population killed by hunters is described. It seems obvious that large-scale banding stations strategically placed throughout the main breeding grounds of waterfowl can be expected to yield valuable data on the effectiveness of waterfowl hunting regulations and a useful index of the annual kill.

There is good reason to believe that, over a period of years, mallard populations are stabilized by an age ratio of about 0.9 young per adult at the end of the hunting season. A preliminary life table based on only 163 birds suggests a considerable shrinkage in the ratio of young to adult after September 1, perhaps from a value of about 1.6. The 55 per cent hatching success for 276 nests studied before 1949 seems to have been sufficient to balance this mortality. The mean clutch size of 7.8 currently reported implies that a considerable amount of renesting is probably taking place in this species.

APPENDIX I

Scientific Names of Birds Mentioned in this Report

(The scientific names of other animals are cited where they appear in the text)

Blackbird, European	<u>Turdus merula</u>
Canvas-back	<u>Aythya valisineria</u>
Cormorant, Double-crested	<u>Phalacrocorax auritus</u>
", European	<u>Phalacrocorax carbo</u>
Dove, Mourning	<u>Zenaidura macroura</u>
Duck, Black	<u>Anas rubripes</u>
", Greater Scaup	<u>Aythya marila</u>
", Lesser Scaup	<u>Aythya affinis</u>
", Ring-necked	<u>Aythya collaris</u>
Finch, House	<u>Carpodacus mexicanus</u>
", Purple	<u>Carpodacus purpureus</u>
Gadwall	<u>Anas strepera</u>
Goose, Canada	<u>Branta canadensis</u>
Gull, Black-headed	<u>Larus ridibundus</u>
Gull, Herring	<u>Larus argentatus</u>
", Lesser Black-backed	<u>Larus fuscus</u>
Hawk, European Sparrow	<u>Accipiter nisus</u>
", Marsh	<u>Circus cyaneus</u>
Heron, Black-crowned Night	<u>Nycticorax nycticorax</u>
", Common	<u>Ardea cinerea</u>
Jay, Blue	<u>Cyanocitta cristata</u>
Lapwing	<u>Vanellus vanellus</u>
Mallard	<u>Anas platyrhynchos</u>
Owl, Barn	<u>Tyto alba</u>
", Great Horned	<u>Bubo virginianus</u>
Pelican, White	<u>Pelecanus erythrorhynchos</u>
Pheasant, Ring-necked	<u>Phasianus colchicus</u>
Pintail	<u>Anas acuta</u>
Redhead	<u>Aythya americana</u>
Robin, (American)	<u>Turdus migratorius</u>
", European	<u>Erythacus rubecula</u>
Song-thrush	<u>Turdus ericetorum</u>
Sparrow, Song	<u>Melospiza melodia</u>
Starling	<u>Sturnus vulgaris</u>
Swallow, Tree	<u>Iridoprocne bicolor</u>
Teal, Blue-winged	<u>Anas discors</u>
", Green-winged	<u>Anas carolinense</u>
Tern, Caspian	<u>Hydroprogne caspia</u>
", Common	<u>Sterna hirundo</u>
Warbler, Yellow Palm	<u>Dendroica palmarum</u>
Wren, House	<u>Troglodytes aëdon</u>

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